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TAXONOMY OF THE GENUS *COLUMBA*

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D. GOODWIN

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TAXONOMY OF THE GENUS *COLUMBA*

By D. GOODWIN

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SYNOPSIS

Previous reviews of the genus *Columba* have grouped together species which lack display plumage on the neck or whose ornamentation is superficially similar. This is believed to have resulted in some false conclusions because such display plumage has been independently lost or become obsolescent in several species. When this is recognized and greater importance attached to basic colour-patterns and geographical distribution a truer picture of relationships within the genus can be arrived at.

INTRODUCTION

THE genus *Columba* includes a large number of medium to large-sized pigeons, widely distributed throughout the world. Peters (1937), for example, lists fifty-two species and does not divide them into sub-genera. The rather inconveniently large size of the genus has often been criticized and the affinities of its members questioned. Ridgway (1916) separated the relatively few northern and central American species into six genera, some of them monotypic. The most important recent revision of the genus is that of Boetticher (1954), who divides it into several sub-genera and corrects some false conclusions of a previous and less comprehensive revision by Miculicz-Radecki (1949).

When re-arranging the very extensive collection of specimens of *Columba* in the British Museum (Natural History) it was found impossible to agree with all of Boetticher's conclusions. The object of this paper, therefore, is a revision of the genus based on examination of the skins in the National Collection and correlated, as far as has been possible, with what is known of the ecology and behaviour of the species of which it is comprised. Emphasis is placed on discussion of those points where my conclusions differ from those of Boetticher. I am indebted to Dr. Dean Amadon of the American Museum of Natural History for the loan of specimens of *Columba albinucha* and *C. pallidiceps*, to Mr. J. D. Macdonald for help and constructive criticism and to Dr. G. Bodenstein, Professor W. F. Hollander and Mr. R. W. Sims for information and discussion on various points.

COLOUR AND COLOUR-PATTERN

Within *Columba* plumage colour ranges from entirely black, with green and purple iridescence, to predominantly pale grey or purplish-chestnut. It is evident that, as in *Ptilinopus* (Cain, 1954) colour-pattern is usually a better guide to relationship than actual colour. One finds striking differences in the colour of the plumage and/or soft parts of the head and neck (the focal area of both sexual attraction and aggressive attack in pigeons) between pairs of sympatric and very closely related species as *C. squamosa* and *C. leucocephala* or *C. rupestris* and *C. leuconota* (see Text-fig. 1).

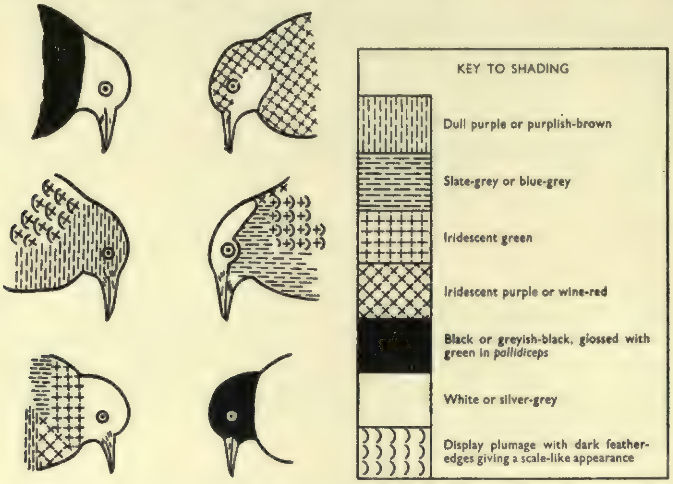
KEY TO SHADING
Dull purple or purplish-brown
Slate-grey or blue-grey
Iridescent green
Iridescent purple or wine-red
Black or greyish-black, glossed with green in *pallidiceps*
White or silver-grey
Display plumage with dark feather-edges giving a scale-like appearance

FIG. 1. Diagrammatic sketches to show differences in head and neck colours between three pairs of sympatric and closely related species. From top left: *pallidiceps* and *vitiensis*, *squamosa* and *leucocephala*, *rupestris* and *leuconota*.

Such differences almost certainly function as isolating mechanisms to inhibit interspecific pairing. Signal markings on wings and tail and specific differences in voice and display-flight serve the same purpose at " longer range ". As with other groups of birds the greatest diversity of signal markings, display plumage and voice is found where there are many related and at least potentially sympatric species and, conversely, a tendency to lose such characters and acquire a dull uniformly coloured plumage in isolated island forms. Lack of signal markings or display plumage in *Columba* seems never to be a primitive character. Examination of the colour-pattern and other characters of the species concerned shows convincingly that their common lack of ornamentation is due to convergence and not to close affinity.

Sexual dimorphism in *Columba* is relatively slight but in most species it is sufficient to enable skins or living birds to be correctly sexed on plumage colour alone. In those species which are predominantly grey males are a purer, bluer grey than females. Purple, chestnut or mauve-pink in males is often duller, absent. or replaced by dull brown in females. Iridescent display plumage (when present) is usually more brilliant in males. Where adults show such differences of plumage similar and homologous sexual differences are found in the juvenile plumage.

ADAPTIVE RADIATION AND RELATIONSHIPS

Adaptive radiation can be misleading at generic level, since once two forms have evolved marked differences of size and structure they are unlikely to be considered con-generic. For example the many Australian bronze-wing pigeons are obviously very close relatives in spite of the taxonomically convenient differences in size and proportions which they have developed in the course of adaptation to different ecological niches. Within *Columba,* as here recognized, the greatest amount of adaptive radiation is found among the Palearctic and Ethiopian species. Similar, but less marked differences are shown among the American species, but here *maculosa,* which otherwise closely parallels the old-world *livia,* has not emancipated itself from the use of trees for resting and breeding.

The question arises whether the New World representatives of *Columba* should be generically separated from the Old World forms. Cumley & Irwin (1944) concluded from their work on the antigenic inter-relationships of the blood cells of *guinea, livia, palumbus, janthina, fasciata, maculosa, picazuro, cayennensis, flavirostris* and *leucocephala* that each of the six American species was more closely related to the other five than to any of the four Eurasian species. Verheyen (1957) considers that skeletal differences warrant the separation of Old and New World forms of *Columba,* both of which groups he further divides into several genera, some of them monotypic. I am not competent to criticize Verheyen's opinions in so far as they are based on osteology, but his decisions placing *guinea* in the monotypic genus *Dialiptila* and generically separating *janthina, vitiensis* and *norfolciensis* are so contrary to the evidence from external taxonomic characters and behaviour-patterns that I hesitate to follow his conclusions without further evidence.

If the New World species are to be generically separated this could be done only on osteological and biochemical characters. Possibly studies currently in progress in America will show that there are constant and significant behavioural differences also and it will be desirable to separate the American from the Old World species. I think, however, that at present it would be premature to do so.

It seems to me best to retain the large genus *Columba* as used by Peters (1937) and Hellmayr & Conover (1942) but to give *Oenoenas* and *Turturoena* sub-generic rank within it. I also think that *Nesoenas* should be given only sub-generic rank within *Columba.* The remaining forms can be relegated to five species-groups. Cain (1954), in his revision of the pigeons in the genus *Ptilinopus,* used the category of the species-group for " an informal natural group of closely related species below the rank of a subgenus, the recognition of which involves no complication of the scientific names of the species contained in it." And that of sub-group for more closely related forms within the species-group. I have followed Cain in the use of these categories which are equally useful for defining relationships of the pigeons in *Columba.* The hierarchy of categories is therefore :

- Genus
  - Sub-genus
    - Species-group
      - Sub-groups (of species group)
        - Superspecies
          - Species
            - Subspecies

There are, naturally, some species whose characters show them to be intermediate between two sub-groups and it has been necessary to allot them somewhat arbitrarily to that with which they seem to have most in common or else to place them in a mono-specific sub-group. All such cases are discussed below. In the following list members of the same superspecies are bracketed together. Subspecies have not been listed but they are discussed under the species headings where they are relevant to specific problems.

THE SPECIES-GROUPS AND THEIR COMPONENT SPECIES

(1) *Oenas Species-group*

Smallish (*oliviae*) to large (*trocaz*) sized columbids inhabiting the Palearctic and Ethiopian regions, one species (*livia*) also occurring in India, and throughout much of the world in a feral state as a result of human introduction. Most species in this group have well developed display plumage on the neck and patterned tails. Sexual dimorphism slight.

(a) *Palumbus Sub-group*

Tail rather long with conspicuous pale central band; breast mauve-pink or salmon-pink.

C. palumbus Linnaeus, 1758
C. trocaz Heineken, 1829
C. bollii Godman, 1872
C. unicincta Cassin, 1859 (1860)

(b) *Oenas Sub-group*

Glossless mauve-pink on head and/or breast, black signal markings on inner wing-coverts (obsolescent in *oliviae*).

C. oenas Linnaeus, 1758
{ *C. eversmanni* Bonaparte, 1856
{ *C. oliviae* Stephenson Clarke, 1918

(c) *Livia Sub-group*

No glossless mauve-pink colour on breast or head. Display plumage on front as well as sides of neck (absent in *leuconota*).

{ *C. livia* Gmelin, 1789
{ *C. rupestris* Pallas, 1811
C. leuconota Vigors, 1831
C. guinea Linnaeus, 1758
C. albitorques Rüppell 1837

(2) *Junioniae Species-group*

Large columbid inhabiting the western Canary Islands of Palma and Gomera. Mantle and wings dark brown and immaculate; tail with broad pale terminal band. Entire neck and breast iridescent but no well differentiated display plumage. One species *C. junioniae* Hartert, 1916.

(3) *Elphinstonii Species-group*

Smallish medium to large-sized columbids inhabiting the Indo-malayan and Ethiopian regions. All except one with unpatterned tails. No signal markings on wings. Most with display plumage on sides and back of neck.

(a) *Arquatrix Sub-group*

Display plumage on hind neck lanceolate. Wing-coverts and/or underparts spotted with white (obsolescent spots in *polleni*).

C. arquatrix Temmink, 1809
C. pollenii Schlegel, 1866
C. hodgsonii Vigors, 1832
C. albinucha Sassi, 1911

(b) *Elphinstonii Sub-group*

Display plumage on hind neck of black feathers tipped white or buff. Iridescent green or purple sheen on neck and mantle. Unpatterned tails, no signal markings on wings. One superspecies.

C. pulchricollis Blyth, 1845 (1846)
C. elphinstonii (Sykes, 1832)
C. torringtoni Bonaparte, 1854

(c) *Punicea Sub-group*

No well differentiated display plumage on neck; wing coverts and body plumage immaculate chestnut or silver contrasting with black primaries.

C. punicea Blyth, 1842
C. argentina Bonaparte, 1855

(d) *Palumboides Sub-group*

Head and neck silver-grey; wings and back dark grey with iridescent feather edges. One species.
C. palumboides (Hume, 1873)

(4) *Janthina Species-group*

Large columbids inhabiting the Pacific regions from Japan to Australia, chiefly on islands. Plumage largely or entirely blackish and highly iridescent. No signal markings on wings; dark unpatterned tails. Not divisible into sub-groups.

C. janthina Temminck, 1830
C. vitiensis Quoy & Gaimard, 1830
C. norfolciensis Latham, 1801

C. versicolor Kittlitz
C. jouyi Stejneger, 1887
C. pallidiceps (Ramsay, 1877)

(5) *Picazuro Species-group*

Small (*rufina*) to medium-large (*maculosa*) columbids inhabiting the nearctic and neotropic regions. Most with display plumage on back and sides of neck and patterned tails.

(a) *Leucocephala Sub-group*

Patch of velvet-like feathers on nape ; well-defined iridescent display plumage on back and sides of neck. Plumage largely dark slate-grey ; wings and tail unmarked.

C. leucocephala Linnaeus, 1758
C. squamosa Bonnaterre, 1792

(b) *Speciosa Sub-group*

Feathers of neck and breast white and golden with dark, iridescent edges ; back, rump and wing-coverts purplish-chestnut (male) or dark brown (female). Tail blackish and unmarked. One species only.

C. speciosa Gmelin, 1789

(c) *Picazuro Sub-group*

Outer wing-coverts edged white ; mantle and wing-coverts brown, tail with ill-defined terminal dark band.

C. picazuro Temminck, 1813
C. corensis Jacquin, 1784
C. maculosa Temminck, 1813

(d) *Fasciata Sub-group*

Parti-coloured tail with broad, pale terminal band. Iridescent green display plumage on hind-neck. One superspecies.

C. fasciata Say, 1823
C. araucana Lesson, 1827
C. caribaea Jacquin, 1784

(e) *Rufina Sub-group*

Small size. Crown and nape iridescent ; ill-defined pale terminal band on tail; plumage mainly vinous-purple.

C. rufina Temminck, 1810

(f) *Flavirostris Sub-group*

No iridescence on head or neck ; plumage largely vinous-purple ; tail dark grey without markings. One superspecies.

{*C. flavirostris* Wagler, 1831
{*C. oenops* Salvin, 1895
{*C. inornata* Vigors, 1827

Sub-genus *Oenoenas*

Small columbids of central and southern America with dark brown and greyish-purple or reddish-purple plumage ; small bills, strongly rounded tails, obsolescent display plumage on hind neck and no markings on wings or tail. Consists of only four species. It seems purposeless to sub-divide further this small and very homogeneous assemblage into sub-groups, which could only be done, if at all, on the shorter tails of two of them, *nigrirostris* and *goodsoni*.

C. subvinacea (Lawrence, 1868)
C. plumbea Vieillot, 1818
{*C. nigrirostris* Sclater, 1859 (1860)
{*C. goodsoni* Hartert, 1902

Sub-genus *Turturoena*

Small columbids inhabiting the Ethiopian region. Bright metallic iridescence on hind-neck. Marked sexual dimorphism except in the island form *malherbii*. One superspecies.

{*C. delagorguei* Delagorgue, 1847
{*C. iriditorques* Cassin, 1856
{*C. malherbii* Verreaux & Verreaux, 1851

Sub-genus *Nesoenas*

Large-sized Mauritian columbid with rounded wings (first primary about equal in length to sixth) and rufous tail. One species.

C. mayeri Prevost, 1843

NOTES ON SPECIES

C. palumbus

The Wood Pigeon is considered by Boetticher (1954) to be most closely related to *torringtoni*, *elphinstonii*, *trocaz* and *junioniae* and to be much nearer to *fasciata* and allied American species than to *oenas* or *unicincta*. He grouped these, and some other pigeons, close together because they all show a high degree of ornamentation on the neck feathers, similar relative lengths of wing and tail and arboreal habits.

Certainly the conspicuous white or cream-coloured patches on its neck give *palumbus* a superficial resemblance to such species as *fasciata* which also have conspicuous white areas in the display plumage of the neck. In its colour-pattern and

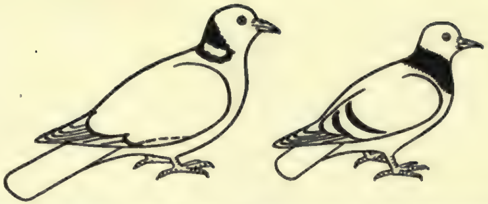

FIG. 2. Diagrammatic sketches to show difference of proportions within the Oenas species-group. Left *C. palumbus*, Right *C. livia*.

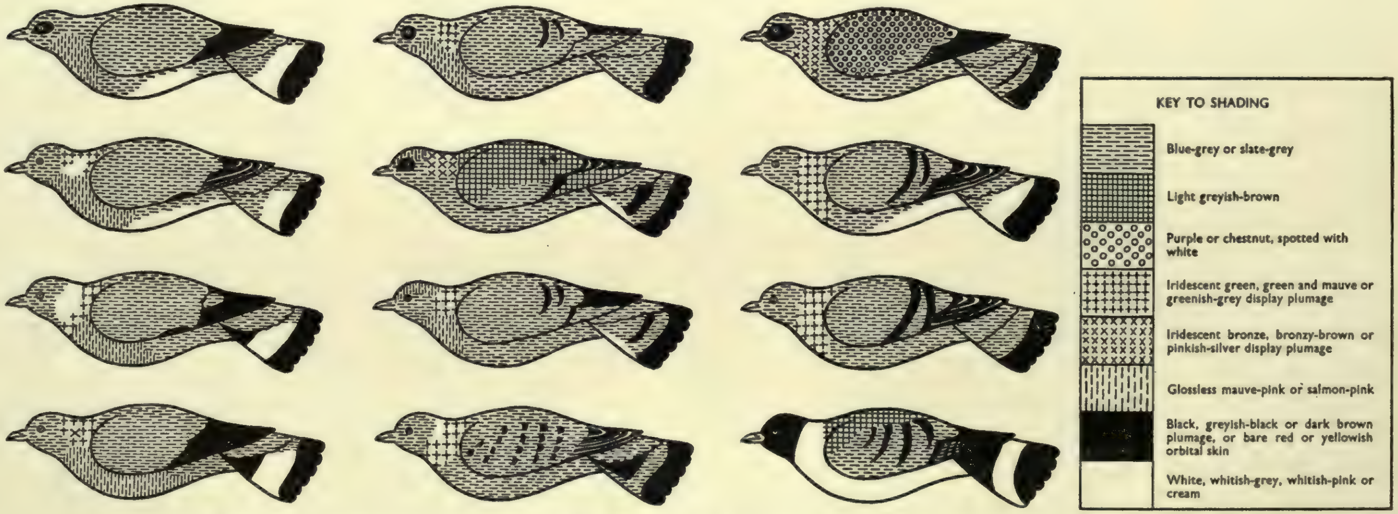
KEY TO SHADING
Blue-grey or slate-grey
Light greyish-brown
Purple or chestnut, spotted with white
Iridescent green, green and mauve or greenish-grey display plumage
Iridescent bronze, bronzy-brown or pinkish-silver display plumage
Glossless mauve-pink or salmon-pink
Black, greyish-black or dark brown plumage, or bare red or yellowish orbital skin
White, whitish-grey, whitish-pink or cream

FIG. 3. Diagrammatic sketches to show range of colours and colour-patterns in the *Oenas* species-group.

C. unicincta.
C. palumbus.
C. trocaz.
C. bollii.

*C. oenas.**
C. oliviae.
*C. eversmanni.**
C. albitorques.

C. guinea.
C. rupestris.
C. livia.
C. leuconota.

* An extensive area of bare orbital skin should be shown on *eversmanni* not on *oenas*.

even in the individual colours, however, it agrees more closely with *unicincta* and *oenas*. The difference in coloration of the display plumage on the necks of *oenas* and *palumbus*, due to the white patches of the latter, can be interpreted as an isolating mechanism (see Sibley, 1957) as can the difference in their advertising calls. The bowing display of *palumbus* is identical with that of *oenas* and its pre-copulatory behaviour is very similar to that of *oenas*, *guinea* and *livia* (see Goodwin, 1956*a*) and differs from that of *fasciata* as described by Whitman (1919). It is true that in some points of structure and deportment *palumbus* bears more resemblance to *fasciata* than to *oenas* but this may be attributed to the fact that *palumbus* and *fasciata* are largely arboreal and obtain much of their food from the tips of slender branches whereas *oenas* is almost entirely a ground feeder. Geographical distribution also seems to favour the linkage of *palumbus* and *oenas*. In my opinion, and excepting obvious derivatives on the Atlantic islands (see *trocaz* and *bollii*), *palumbus* has closest affinities with *unicincta* and is nearer to *oenas* than it is to *pulchricollis* or *fasciata* or to their close allies. At the same time its undoubted resemblance to these latter emphasize the difficulties of generically separating the Eurasian and American groups of *Columba*.

C. trocaz

The Madeiran Pigeon appears to be a fairly recent derivative of *palumbus*. In its voice and bowing display it closely resembles that species and in appearance it differs only in its slightly darker coloration, in lacking the white signal markings on the wings and in its slightly longer legs and more sloping forehead. As, however, it would seem to have diverged sufficiently not to have interbred with later Wood Pigeon invaders, now distinguished racially as *C. palumbus maderensis*, it has to be accorded specific rank.

C. bollii

Bolle's Pigeon is considered by Peters (1937) and others to be conspecific with *trocaz*. Both appear to be derivatives of *palumbus* but evidence suggests that they did not share a common ancestry subsequent to their differentiation from the parent stock. Although both have lost the white wing patch of *palumbus* the white neck patch has modified in different directions in each. In *trocaz* it has become a dull silvery grey and increased in area whereas in *bollii* it has become a small glossy brown mark. Since *trocaz* cannot now be considered conspecific with *palumbus* it seems better to give *bollii* specific status also.

C. unicincta

Boetticher considers the Afep Pigeon to be a relatively primitive species, most closely related to *maculosa*, because it lacks display plumage on the neck. It seems to me much more likely that loss of display plumage has occurred at a relatively late stage in the evolution of both species and does not indicate any close phylogenetic relationship between them. In its general colour pattern *unicincta* agrees fairly closely with *palumbus* and its tail markings are identical with those of that species. Two features in which *unicincta* differs from *palumbus* are in its pale-edged wing-coverts and in its grey feet and bill. Since, however, these features, like the lack of iridescence on the neck, are similar to those in juveniles of *palumbus* I do not think they diminish the likelihood of close phylogenetic relationship of *unicincta* and *palumbus*, which their other features, including the little that has been recorded about the behaviour and ecology of *unicincta*, seem to indicate.

C. oenas

The Stock Dove is usually considered to be much more closely related to *livia* than to *palumbus* but in fact it forms a connecting link between the two in its taxonomic characters as well as in its ecology and behaviour (Goodwin, 1956*a*). Thus it agrees with *palumbus* in the distribution of the display plumage on its neck, in its glossless mauve-pink breast and in the form of its bowing display, but its wing and tail markings and its proportions are closer to *livia*. In view of the intermediate position of this, the type species of *Columba*, generic separation of " wood pigeons " and " rock pigeons " becomes untenable.

C. eversmanni

Eversmann's Stock Dove is extremely close to *oenas* in appearance, differing only in its smaller size, yellow irides and in having the head as well as the breast mauve-pink, or with a strong mauve-pink tinge, and in sometimes having a white instead of a grey rump. I concur with Peters in thinking that the evidence at present available warrants their both being considered full species. Stuart Baker (1928) put *eversmanni* as a race of *oenas* stating that " intermediate forms are not infrequent ". He gave no evidence for this other than mentioning some grey-rumped *eversmanni* having been obtained in Afghanistan. Except in this one feature grey-rumped individuals do not resemble *oenas* any more closely than do white-rumped ones. Stuart Baker's further remarks about the affinities of the two show that he knew little about the behaviour and ecology of *oenas*. The breeding range of *eversmanni* as indicated by Dementiev *et al.* (1951) has a considerable overlap with that of *oenas*. That they retain their respective characteristics where they are, apparently, sympatric, is evidence of their specific status.

C. oliviae

The Somaliland Pigeon can be regarded as forming a superspecies with *eversmanni*. The differences between them can be explained by the adaptation of *oliviae* to its torrid desert habitat. As well as acquiring a paler and browner coloration it has lost the black wing bars, probably quite recently, as many specimens show a few blackish flecks where these are in *eversmanni*. The loss of these signal markings may have resulted from a need for more perfect camouflage or simply to lack of selection for them subsequent to isolation from other closely related species. Unfortunately nothing appears to have been recorded of the behaviour or breeding habits of this species. In spite of its alternative vernacular name of " Somali Rock Pigeon ", *oliviae* is no more closely related to *livia* than are *eversmanni* or *oenas*.

C. albitorques

The White-collared Pigeon has a white neck ring like that of *fasciata* and acuminate neck feathers like *arquatrix*. But as it resembles these species in no other respects it is highly unlikely that these likenesses indicate close relationship. Its tail pattern and the black markings on its wings seem to indicate relationship to *oenas* and *livia*. Taibell (1954) describes a bowing display like that of *oenas*. The lack of strong contrast between the black wing markings and their dark grey background, the slight degree of iridescence of the neck feathers and the partially concealed white wing patch may indicate that *albitorques* is at a stage of evolution where it is beginning to lose some of its display and signal markings, presumably as a result of being now ecologically isolated from related species. On the whole the appearance and taxonomic characters of this pigeon suggest a rather closer relationship with *livia* and *guinea* than with *oenas* and I have, accordingly, placed it in the *livia* sub-group.

C. guinea

It is fairly certain that the Speckled Pigeon is a close relative of *livia* (see Goodwin, 1956 and 1956*a*) in spite of their differences of colour. They resemble each other in having display plumage on the front as well as on sides and back of the neck and in having the feathers of this display plumage bifurcated; there are also many close resemblances of voice and behaviour. On the evidence of the blood antigens Cumley & Irwin showed that biochemically *guinea* is closer to *palumbus* than it is to *livia* or *oenas*. This is supported by two points of behaviour—its calls and postures immediately after copulation and its methods of fighting. Thus what is known of this species emphasizes the essential homogeneity of the *oenas* species-group in spite of the rather considerable, if somewhat superficial, taxonomic and behavioural variations within it. I think, however, that in sub-dividing this group *guinea* should be put in the same sub-group as *livia*.

C. leuconota

The Snow Pigeon's plumage and general habits suggest a close relationship with *livia* and *rupestris*. The great differences in colour of the head and neck between *leuconota* and *rupestris* is almost certainly to be considered as an isolating mechanism and of little importance as an indicator of phylogenetic disparity. The same may be true of the apparently considerable difference between the voice and bowing display of *leuconota* (Newman, 1911) and that of *livia*. The black and white pattern on the tail of *leuconota* appears different from that of *livia* and other allied species but is essentially similar, the differences being due to a reduction of the black terminal band and an extension of the black basal area on the outer rectrices.

C. livia

The Rock Pigeon gives an impression of standing far apart from *palumbus* in appearance and behaviour. Boetticher (1954) indeed puts them as the terminal twigs on the two mutually diverging main branches of his family tree of *Columba*. The differences of form, behaviour and coloration shown by *livia* are largely due to its adaptations to nesting and sheltering in caves and rock fissures and feeding in open tree-less country. In fact I think that *livia* and *palumbus* are fundamentally much alike and that they represent the extremes in a single rather large species-group. Although *livia* now occurs in some moderately wooded regions it almost certainly evolved in a treeless or almost treeless environment. Its points of resemblance to *rupestris, guinea* and *oenas* are discussed under those species.

C. rupestris

The Blue Hill Pigeon is usually accorded specific rank although Austin (1948) put it as a race of *livia* but without giving reasons for this decision. Over most of their range the two are allopatric, *rupestris* replacing *livia* in the higher and colder parts of central and eastern Asia. The differences between them are certainly such as suggest racial rather than specific status. *Rupestris* has a proportionately smaller bill and a reduced amount of melanin in the plumage resulting in a white instead of a grey central bar in the tail, smaller black wing bars, paler grey ground colour and less intensely iridescent display plumage ; all differences such as might be expected in a race inhabiting a colder climate. With the possible exception of the white tail bar none of these cause as great difference in appearance as exists, for example, between *C. livia gymnocyclus* and *C. l. dakhlae* or *C. l. livia* and *C. l. intermedia*. In its habits and ecology (Schafer, 1938) *rupestris* apparently differs in no essentials from *livia*.

These facts suggest that the two are conspecific. On the other hand *rupestris* is said to associate with *livia* in parts of northern India (Stuart Baker, 1913) and it is potentially in contact with feral specimens of *livia* in many parts of its range. La Touche (1934) shot a specimen of *C. livia intermedia* (sic) out of a flock of *rupestris* in eastern China. The voice of *rupestris*, as described by Salim Ali (1949), would appear to differ much from that of *livia*. The evidence is thus conflicting. La Touche considers that the occurrence of mixed flocks suggest that *rupestris* and *livia* interbreed but this might equally well be evidence to the contrary. If, as is likely, the term " mixed flock " has been applied to aggregations of *rupestris* and (? feral) *livia* at feeding grounds then such associations are of no significance either way. There are no specimens from among the many from North India and the Himalayas in the National Collection that appear to be hybrids or intergrades between the two. It must be admitted, however, that such birds might be difficult to detect, unless they were intermediate in coloration of the tail. Until the matter can be investigated more conclusively it seems best to accept the majority opinion that *rupestris* is a full species. Since the evidence suggests strongly that, at least as far as genuinely wild individuals are concerned, *livia* and *rupestris* are allopatric when breeding they should, I think, be considered members of a superspecies.

C. junioniae

The coloration and size of the Laurel Pigeon suggest relationship to *palumbus*. On the other hand the colour-pattern of its tail is similar to that of *albinucha* and *fasciata*. Meade-Waldo (1889) described it as having a very distinctive gait when walking on the ground and a " soft, flopping flight " which was unlike that of any other pigeon known to him. He found that on the Island of Gomera, in the Canaries, it kept mainly to scrub-covered slopes at relatively low altitudes, being replaced in the high mountain forest by *C. bollii*. It lays one egg to a clutch. The Laurel Pigeon seems most likely to be either an offshoot from primitive palearctic *Columba* stock prior to its subsequent speciation or an early offshoot from *palumbus*. It is impossible to do more than guess at its affinities from an examination of skins and the little that has been recorded of its behaviour. A detailed comparison of its anatomical and behavioural characters with those of, at least, *palumbus, fasciata* and *albinucha* will probably be necessary before its true relationships can be ascertained.

C. arquatrix

Nominate *arquatrix* with a purple head, silver-grey nape and yellow bill and legs

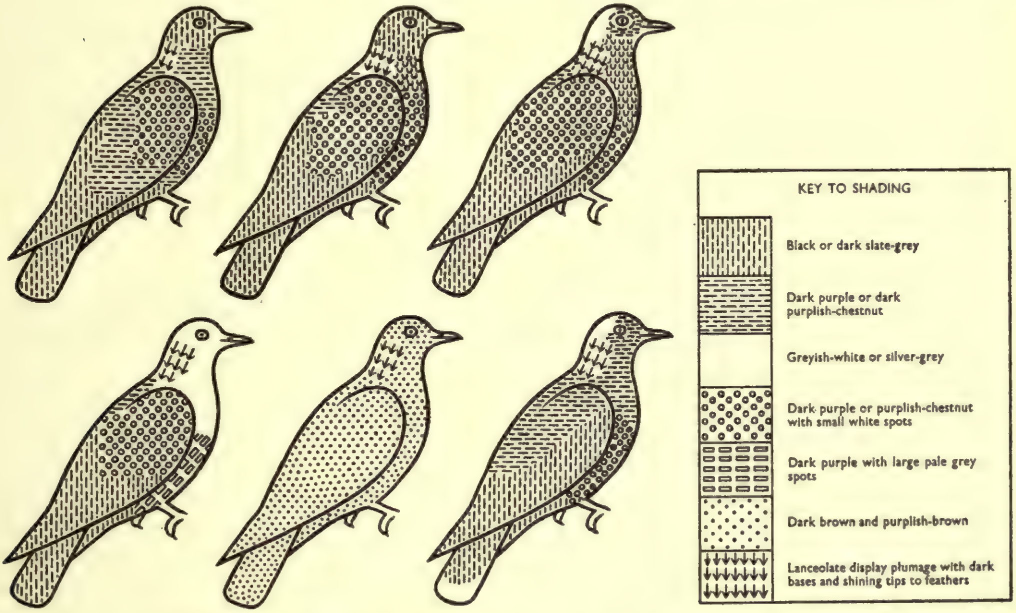
KEY TO SHADING
Black or dark slate-grey
Dark purple or dark purplish-chestnut
Greyish-white or silver-grey
Dark purple or purplish-chestnut with small white spots
Dark purple with large pale grey spots
Dark brown and purplish-brown
Lanceolate display plumage with dark bases and shining tips to feathers

FIG. 4. Diagrammatic sketches to show colours of the *Arquatrix* sub-group. Left to right: *a. thomensis, a. sjostedti, a. arquatrix* and (bottom) *hodgsoni, polleni* and *albinucha*.

has always been considered, rightly in my opinion, conspecific with *sjostedti* from the Cameroon Mountains, which has an entirely dark grey head, red orange-tipped bill and dark purplish legs and feet. The Sao Thomé representative, *thomensis*, is, however, currently given specific rank. It should, I think, be put as a race of *arquatrix*. In plumage it is just a dull version of the latter with the spotting on wing-coverts and undersides and the lanceolate display plumage on the neck showing, apparently, the beginning of that obsolescence of markings that so often takes place in island forms. It otherwise shows characters of both mainland forms, having an entirely dark grey head like *a. sjostedti* but yellow legs and bill like *a. arquatrix*. It has a somewhat longer tail than either mainland form but this alone does not, in my opinion, warrant its specific separation from them.

*C. polleni**

In spite of its almost uniform dark brown plumage *polleni* is also a representative of *arquatrix*. Although, presumably in the course of long isolation on the Comoro Islands, it has lost the rich colours of *arquatrix* it still retains lanceolate display plumage on the hind neck and the yellow legs and bill. Of three skins in the National Collection one shows faint pale spots on the underparts exactly similar to, though less pronounced than the spots of *arquatrix*. It has, however, reached a degree of differentiation from *arquatrix* that justifies, in my opinion, its specific rank, though it should be considered as forming a superspecies with *arquatrix* and *hodgsoni*.

C. hodgsoni

Verheyen (1955) considers this Indian species conspecific with *arquatrix*. That they are geographical representatives of the same stock cannot be doubted but *hodgsoni* differs from *arquatrix* in several minor points of coloration of plumage and soft parts and in its much greater sexual dimorphism. In view of this and of their wide geographic separation I think it is better to give them specific rank as members of the same superspecies.

C. albinucha

In coloration, colour-pattern and display plumage the White-naped Pigeon very closely resembles *arquatrix*. It differs in having red bill and feet, a patterned tail with conspicuous pale terminal bar and in lacking the white spots on the wing-coverts, although its underparts are spotted in the same manner as those of *arquatrix*. It is also a little smaller. The two are sympatric but their ecology and habitat preferences differ (Van Someren, 1949). Nothing seems to have been recorded of the displays, nesting or clutch-size of *albinucha*. Although there can be no doubt that they should be regarded as good species, the resemblances between *albinucha* and *arquatrix* are almost certainly due to close phylogenetic affinity and not to convergence.

C. elphinstonii, C. pulchricollis and *C. torringtoni*

Although differing in size and coloration these three forms all resemble each other in colour-pattern, form of display plumage and (so far as is recorded) in habits and ecology. It is difficult to decide whether it is best to treat them as races of a single species or as members of a superspecies. Their ranges nowhere overlap and they have, presumably, been long isolated from contact with each other. As they have always been accorded specific rank it seems to me best to regard them as members of a superspecies.

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* Through the kindness of Mr. C. W. Benson I have recently been able to examine the fine series of *polleni* collected on the B. O. U. Centenary Expedition to the Comoro Islands. These specimens show that the unsexed skins I had previously seen were all females and all somewhat "foxed". In fact males are a brownish purple on head, upper mantle and breast and the dark brown parts of both sexes are suffused with grey, especially on the rump. They thus resemble *arquatrix* more closely than I had thought and Mr. Benson informs me that the calls of the two are similar ; possibly identical. I, therefore, now consider that *polleni* should be treated as a race of *arquatrix* and not as a separate species.

C. punicea

The Purple Wood Pigeon most closely resembles *argentina* in colour-pattern although its purplish-chestnut body colour gives it a very different superficial appearance. This species is said sometimes to lay one and sometimes two eggs per clutch (Stuart Baker, 1913). If this is really the case—no one other than Stuart Baker appears to have found nests with more than one egg—this is an interesting intermediate condition between the species laying one egg and those laying two.

C. argentina

The Silver Pigeon shows a striking resemblance to the Pied Imperial Pigeons in colour and colour-pattern. Boetticher (1954) considered it more closely related to *Ducula* than to *Columba*. I have been unable to find any description of the anatomy of this pigeon which would show whether its stomach and intestines are of *Ducula* or *Columba* type. From its plumage characters, I think, however, that it is rightly placed in *Columba*. It shows the same type of sexual dimorphism—female a slightly duller and browner grey—in plumage colour as do other grey *Columba* species. It resembles *punicea* in the colour-pattern of its wings although the coloration of the two is different. Superficially the tail appears to be similarly marked to that of the Pied Imperial Pigeon but the pattern on the outer retrices (see Text-fig. 5) is quite different. I think, therefore, that *argentina's* resemblance to the pied *Ducula* species is due to convergence and that it is best regarded as a rather aberrantly coloured member of the *Elphinstonii* species-group. It is another example of a *Columba* species which appears to have lost the display plumage on the neck, a point compatible with its presumed affinity to *punicea* which appears to show a regressional stage of this display plumage.

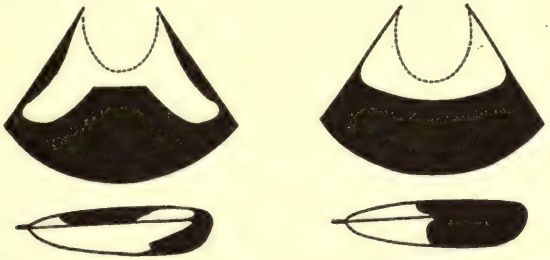


FIG. 5. Diagrammatic sketches to show colour-patterns of tails and outermost tail feathers of left, *Ducula bicolor*; right, *Columba argentina*.

C. palumboides

In appearance, at least of the skin, the Andaman Wood Pigeon suggests a link between the *Elphinstonii* and *Janthina* species-groups. It seems likely to be nearer to the former on geographical grounds. Hume (1867) who collected some specimens and had a captive bird under observation was impressed by its " mode of holding itself and its broad substantial body " which he considered argued relationship to *Ducula* rather than to *Columba*. This may not be of importance as in so far as it is adapted to an arboreal life ; any large pigeon is bound to show some resemblance to *Ducula* as indeed does the common Wood Pigeon *palumbus*. A comparison of the alimentary tracts and a comprehensive study of the foods taken by this and other very arboreal *Columba* species with those of the *Ducula* species living in the same regions would be of great value.

C. janthina

The Black or Japanese Wood Pigeon and *C. vitiensis*, seem best considered as members of a single superspecies. *C. j. nitens* with its distinctive purple-brown head is somewhat intermediate, but in most respects is closer to nominate *janthina* than to any race of *vitiensis*. Stresemann (1939) suggests New Guinea as the place of origin of these forms and gives a map of their distribution and the probable directions of their former spread from the Papuan regions.

C. vitiensis

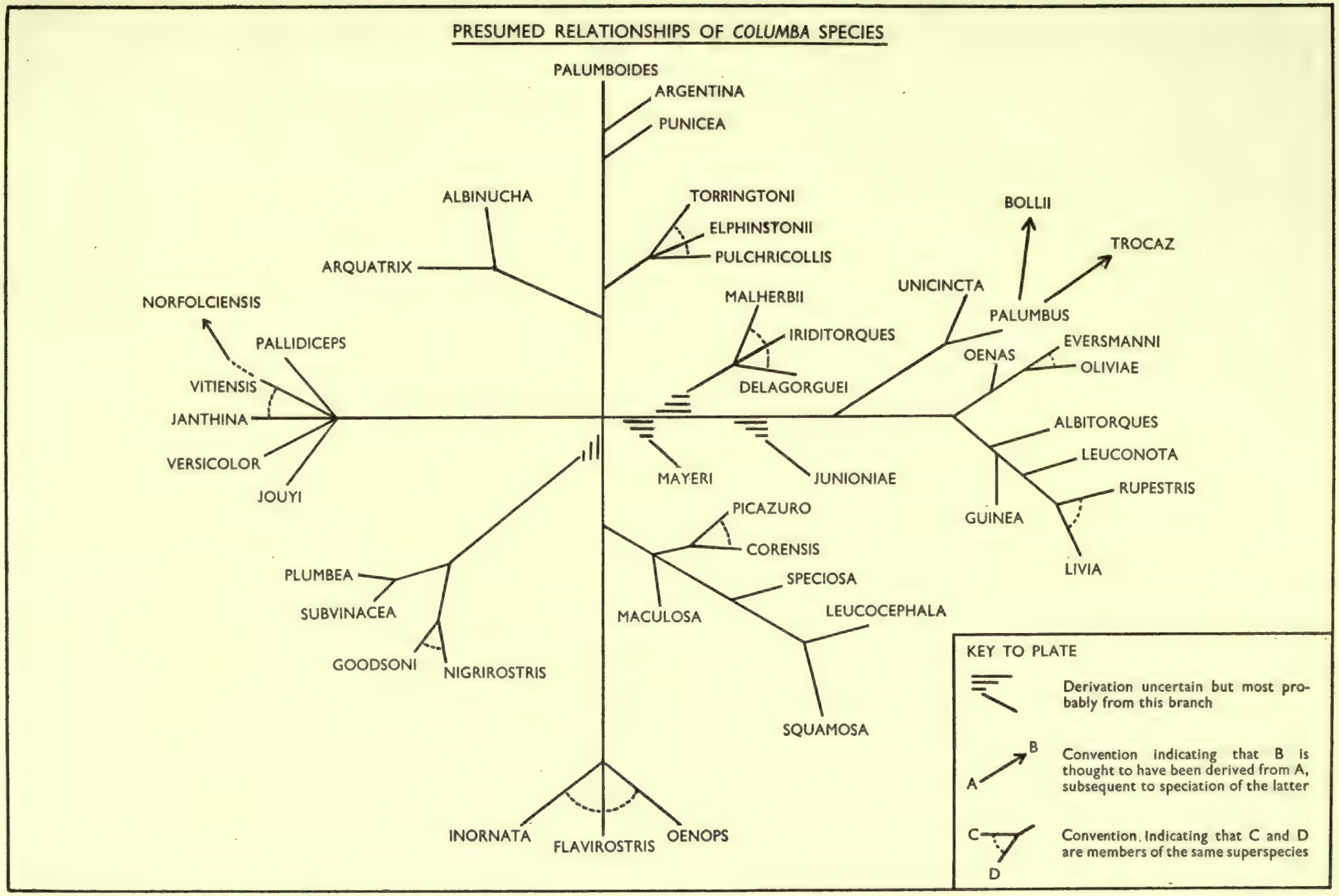
Although generally arboreal, so far as is known, *C. v. halmaheira* has been recorded nesting on the ground among thick cover (Warner, 1949) and Mr. I. C. J. Galbraith informs me that the natives on the Solomons told him that ground nesting was not infrequent in this species. In its bowing display (Newman, 1910) the bird moves rather slowly and does not erect its tail.

C. norfolciensis

This species appears to be a derivative of *vitiensis*. Males differ strikingly from the parent species in having the head and underparts white, or, in new plumage, creamy buff with a pink tinge. Females, however, have these parts whitish-grey or greyish-buff with some iridescence on the crown of the head and the pale throat—as in *vitiensis*—almost pure white and fairly clearly demarcated. Whether *norfolciensis* merits specific recognition is arguable but in view of the great difference in the appearance of the males, which makes it highly likely that if at some future period it were to invade the range of *vitiensis* or vice versa the two would not interbreed, and the nomenclatorial changes that would be involved, it seems preferable to accord it specific rank within the same superspecies.

C. versicolor

This extinct species appears to have been a very close relative of *janthina*. Kuroda (1925) considers it a race of *janthina*. Both forms occurred, however, on the Bonin Islands and I think therefore that Peters (1937) was right to give them specific rank in spite of their obvious affinities in form and coloration.



PRESUMED RELATIONSHIPS OF *COLUMBA* SPECIES

PALUMBOIDES
ARGENTINA
PUNICEA
TORRINGTONI
ELPHINSTONII
PULCHRICOLLIS
ALBINUCHA
ARQUATRIX
NORFOLCIENSIS
PALLIDICEPS
VITIENSIS
JANTHINA
VERSICOLOR
JOUYI
MALHERBII
IRIDITORQUES
DELAGORGUEI
UNICINCTA
BOLLII
TROCAZ
PALUMBUS
OENAS
EVERSMANNI
OLIVIAE
ALBITORQUES
LEUCONOTA
RUPESTRIS
GUINEA
LIVIA
MAYERI
JUNIONIAE
PICAZURO
CORENSIS
SPECIOSA
LEUCOCEPHALA
MACULOSA
SQUAMOSA
PLUMBEA
SUBVINACEA
GOODSONI
NIGRIROSTRIS
INORNATA
FLAVIROSTRIS
OENOPS
KEY TO PLATE
Derivation uncertain but most probably from this branch
A
B
Convention indicating that B is thought to have been derived from A, subsequent to speciation of the latter
C
D
Convention. Indicating that C and D are members of the same superspecies

NOTE: the species *hodgsoni* should have been shown branching from the same line as *arquatrix*, with which it forms a superspecies.

C. jouyi

Kuroda (1925) considers *jouyi* conspecific with *janthina*. Its distribution as given by him overlaps with nominate *janthina* on Okinawa. Jahn (1940) does not, however, record *jouyi* from Okinawa. Besides the large silver patch on its hind-neck and mantle—which presumably functions as a recognition mark and probably also as an isolating mechanism—*jouyi* is a larger, longer-tailed bird and shows only slight traces of iridescence other than on the neck and nape. I therefore think it best to follow Peters in giving *jouyi* specific status.

C. pallidiceps

The Yellow-legged Pigeon appears to be a derivative from *vitiensis* stock. It now overlaps *C. vitiensis halmaheira* on some of the Solomon Islands (Mayr, 1934) although only *pallidiceps* occurs in New Britain, where it perhaps originated. Although much alike in general appearance the two differ strikingly in the coloration of the head, silver-grey in *pallidiceps*, dark purple with a white throat in *vitiensis*; and in the feet, which are red in *vitiensis* and yellow in *pallidiceps*. The coloration of *pallidiceps* is suggestive of that of *norfolciensis* (q.v.) whose close relationship to *vitiensis* is beyond doubt. It would be interesting to know if the difference in leg colour between the two serves in any way as an isolating mechanism. It would seem rather unlikely particularly as it is not correlated with any difference in bill colour, which is mainly red in both species. In other pairs of *Columba* species (e.g. *arquatrix* and *albinucha*) in which one has yellow and one red legs there is a correlated difference in bill colour.

C. leucocephala

The White-crowned Pigeon is very closely related to the Red-necked Pigeon *C. squamosa*. Both have the same highly-developed and beautifully (but differently) coloured display plumage on the back and sides of the neck, are of similar size and inhabit the same geographical areas. They may, however, be ecologically isolated as in Cuba (Barbour, 1943) ; *leucocephala* is a coastal and *squamosa* a highland form. The striking difference in coloration of the head, eyes and display plumage in these otherwise almost identical forms suggests that these differences function or have functioned as isolating mechanisms.

It seems probable that this pigeon lays but one egg to a clutch (Wetmore and Swales, 1931) in spite of an earlier statement (Gundlach, 1874) that it lays two.

C. squamosa

The close relationship between the Red-necked and White-crowned pigeons has been discussed under *leucocephala*. The sexual dimorphism in *squamosa* is much less than in *leucocephala* but readily apparent when skins in a like state of plumage are compared. Probably this pigeon also lays only one egg (Wetmore, 1927) in spite of earlier statements (Gundlach, 1874) to the contrary.

C. speciosa

The Scaled Pigeon appears to be fairly close to *squamosa* and *leucocephala*. In some respects its plumage is intermediate between that of these species and of *picazuro* but I do not agree with Verheyen that *speciosa* and *picazuro* should be generically separated from *squamosa* and *leucocephala*. In *speciosa* the dark edgings to the feathers are found throughout most of its plumage but are intensified in contrast and brilliance on the neck, thus giving a suggestion of the condition obtaining in *leucocephala* and *squamosa*. The Scaled Pigeon shows strong sexual dimorphism, the male having the mantle and wing-coverts rich purple (fading to chestnut) whereas those of the female are dull brown.

C. picazuro

The Picazuro Pigeon has the display plumage on the neck less highly developed than in *leucocephala* and *squamosa* but of an essentially similar kind. According to Hudson (1920) its habits, gait and behaviour are similar to those of *palumbus* but except for a vivid contrast of its gait on the ground with that of *maculosa* he gives no details. Hudson said that it lays two eggs, Venturi (see Hartert, 1909) that sometimes one and sometimes two eggs are laid. Wetmore (1926) found a nest with one egg. He also said that the display flight is like that of *livia*, a rather surprising fact in an essentially woodland species.

C. corensis

The Bare-eyed Pigeon can be considered as forming a superspecies together with *picazuro*. Its main differences, the much paler coloration and the very extensive amount of bare orbital skin, are probably adaptations to the hot, coastal areas where it lives.

C. maculosa

I think the Spotted Pigeon is most closely related to *picazuro*. It has evidently become more fully adapted to feeding on the ground in open country. Its resemblance in wing/tail proportions and gait to *livia* is almost certainly due to convergence in feeding habits. This is another species which has no display plumage on the neck, probably having lost it at a relatively recent date. If so, no close relationship to other species sharing this negative character is indicated.

C. fasciata

The Band-tailed Pigeon is reminiscent of *C. arquatrix* in its yellow bill and feet. The pattern of the bill is unusual in adult *Columba* but very much like that of *Columba* nestlings, only the dark sub-terminal band having " spread " to the tip of the bill and the lighter base turned bright yellow. The copulation ceremony of this species (Whitman, 1919) evidently differs in several details from that of European *Columba* species.

C. araucana

Although the Chilean Pigeon is very closely related to the southern form of the Band-tailed *C. fasciata albilinea* it has, I think, diverged sufficiently to be given specific rank. Besides the plumage differences (purplish-maroon on mantle and scapulars) it has a dark bill and red legs. It can be considered as forming a superspecies together with *fasciata* and *caribaea.*

C. caribaea

The Jamaican Band-tailed Pigeon is clearly derived either from *fasciata, araucana* or from some comparatively recent form ancestral to them both. In plumage it differs from *fasciata* only in being paler, in having lost the white neck-ring and having less well developed iridescent display plumage on the neck. It differs also in having, like *araucana,* a dark bill and red legs.

C. cayennensis

The Rufous Pigeon is intermediate in many respects between the members of the "*fasciata*" superspecies and those of the superspecies "*flavirostris*". It resembles the former in the colour-pattern of its tail feathers and in having display plumage on the hind neck but in its other plumage characters it is closer to *flavirostris.* Little or nothing seems to be recorded about its breeding habits in the wild but two clutches of one egg each were laid by captive specimens (Newman, 1910).

C. flavirostris

The Red-billed Pigeon forms a superspecies together with *oenops* and *inornata.* All three completely lack display plumage on the neck thus presenting a superficial resemblance to the *Oenoenas* species.

C. oenops

This is the Peruvian representative of *flavirostris.* In appearance it differs only in the colour of its bill, which is yellow, or yellow tipped with black, instead of pink and whitish. Also the males have a larger area of ruddy purple on the plumage of the upper parts but females and juveniles are intermediate in this respect between males of their own species and *flavirostris.*

C. inornata

This island representative of *flavirostris* differs only in its larger size, black bill and grey, instead of red, orbital skin.

The Sub-genus *Oenoenas*

Salvadori (1893) characterized this sub-genus as having "general plumage, brown, more or less vinous, and with no light spots on the neck, but sometimes with concealed reddish spots, more or less obsolete, on the hind-neck". Actually the "reddish spots" are appreciably lighter than the adjacent areas of the feathers that show them and these pigeons also have, as pointed out by Ridgway (1916), rather small bills and strongly rounded tails. Ridgway gave them, and others less deserving, full generic rank but subsequent authorities (Peters, 1937; Hellmayr & Conover, 1942; de Schaunsee, 1948) put *Oenoenas* into the synonymy of *Columba*.

The four species concerned, *plumbea*, *subvinacea*, *nigrirostris* and *goodsoni* are all closely related and are more sharply differentiated than any others within *Columba*, *mayeri* excepted. I do not concur with Boetticher in considering them to be closely related to *caribaea* or that their dull concolorous plumage represents the retention of a primitive condition. The *Oenoenas* species differ from other American pigeons (except for the quite differently coloured *speciosa*) in lacking grey on the rump, which is concolorous with the mantle and wings or nearly so. The more or less obsolescent pale or bronzy-red markings on the feathers of the hind-neck are more prominent in females than in males, which suggests that so far from representing display plumage in process of acquisition, as Boetticher suggests, the reverse is the case. The obsolescent display plumage and general dull coloration of *Oenoenas* seems to be, in the evolutionary sense, a relatively recent development, not the retention of primitive characters.

Oenoenas is most probably an early offshoot from the other American *Columba* that has diverged considerably from the parent stock. Its sombre, concolorous dress with complete lack of signal markings and obsolescent display plumage presumably evolved as a consequence of increased predator pressure consequent on smaller size and/or increased reliance on vocal differences as isolating mechanisms.

C. plumbea and *C. subvinacea*

Only the fact that these pigeons appear to be sympatric in parts of their range. makes it possible—on present knowledge—to consider them as specifically distinct. Whilst the slight differences of colour and bill size make it possible to identify most specimens, it is difficult to believe that they could be sufficient to act as isolating mechanisms for the birds themselves. Presumably vocal and behavioural differences exist, but they do not appear to have been recorded. A few specimens in the National Collection are intermediate in character between *plumbea* and *subvinacea* but it is impossible to say whether these are hybrids or merely individuals whose slight aberrancy is towards the characters of the other species.

C. nigrirostris and *C. goodsoni*

These can certainly be regarded as forming a single superspecies. They may well be conspecific but since their taxonomic differences are at least as great (or one might better say no less) than those of *plumbea* and *subvinacea*, it seems better to grant them specific rank until more is known about them.

The Sub-genus ***Turturoena***

This is comprised of three allopatric species *delagorguei*, *iriditorques* and *malherbei* which replace one another geographically and can be considered as forming a single superspecies. Salvadori (1893) separated *Turturoena* generically from *Columba* on its smaller size, hind neck with bright metallic colours and the sexes being often very dissimilar. Subsequent authorities have disagreed about its status, Peters (1937) placing it in the synonymy of *Columba* and Cave & Macdonald (1955) and Mackworth-Praed & Grant (1952) giving it full generic rank. I think, personally, that the differences do not merit more than sub-generic rank within *Columba*.

Boetticher considers that *Turturoena* is more closely related to *Aplopelia* than to *Columba*. Certainly all three species have a similar distribution of iridescence to that of the *Aplopelia* species (but one found also in some species of *Columba*, and other pigeons) and a similar degree and type of sexual dimorphism. However, in my opinion, they show more affinities to the *Columba* species, not only in their general appearance but also in their colour-patterns which much resemble those found in *palumbus* and allied species. Mr. R. E. Moreau informs me (in litt.) that the cooing of *delagorguei sharpei* in Tanganyika reminded him very much of that of the Wood Pigeon, *palumbus*.

The Sub-genus ***Nesoenas***

Salvadori (1893) placed the Mauritius Pigeon, *C. mayeri*, in the monotypic genus Nesoenas because of its more rounded wing, with the first primary about equal in length to the sixth, and its rufous tail. In coloration this pigeon does not closely resemble any other *Columba* but its colour-pattern shows some resemblance to the *oenas* species-group, from which it may possibly be an offshoot. Fortunately this species is not extinct as was at one time feared so it is possible that studies of it that will serve to indicate its affinities may yet be made. In the meantime I think it is better to put *Nesoenas* as a sub-genus within *Columba* than to afford it generic rank.

SUMMARY

This paper revises the genus *Columba*. The taxonomic and behavioural characters of the species are discussed in reference to their probable affinities.

The absence or obsolescence of the display plumage on the neck is never a primitive character in *Columba* but one that has evolved independently in several species.

Oenoenas, *Turturoena* and *Nesoenas* are given sub-generic rank. It does not seem feasible to further sub-divide the genus. There are indications that the American species may prove separable on anatomical and biochemical criteria although they cannot be separated on external characters.

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A REVISION OF THE PLATYSEIINAE (MESOSTIGMATA: ACEOSEJIDAE)

BASED ON MATERIAL IN THE COLLECTIONS OF THE BRITISH MUSEUM (NATURAL HISTORY)

G. OWEN EVANS and K. H. HYATT

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INTRODUCTION

The family Aceosejidae is divided into two subfamilies, Aceosejinae and the Platyseiinae, on the basis of the chaetotaxy of the gnathosoma and the tarsi of legs II–IV (Evans, 1957). The classification of the Aceosejinae has been outlined by Evans (1958) but no revisionary work has yet been undertaken on the Platyseiinae which, at present, contains six genera, namely, *Sejus* C. L. Koch, 1843, *Cheiroseius* Berlese, 1916, *Platyseius* Berlese, 1916, *Episeius* Hull, 1918, *Zerconopsis* Hull, 1918, and *Episeiella* Willmann, 1938.

Koch (1836) originally assigned a number of species to the genus *Sejus* but did not designate the type species of the genus, *Sejus viduus* C. L. Koch, until 1843. Berlese (1892) accepted Koch's wide concept of the genus and in 1913 proposed the family Seiidae for its reception together with eight other genera. Later in 1916, the same author revised his concept of the Seiidae and stated that *Seius* (=*Sejus*), with *Sejus togatus* C. L. Koch as the type, was not confamilial with the other genera he had included in the family in 1913. Thus, the family Seiidae was reserved for those species having the general characteristics of *Sejus togatus*. Subsequent workers (Vitzthum and Trägårdh) accepted Berlese's definition of *Sejus* and the family became established in the literature until 1936 when Oudemans noted the error in considering *S. togatus* to be the type of *Sejus*. Consequently *Sejus* Berlese *nec* Koch became a synonym of *Liroaspis* Banks in spite of Trägårdh's remark that "this incident offers yet another strong argument in favour of establishing *nomina conservanda*" (Trägårdh, 1946). We are following Sellnick (see Willmann, 1953) who considers *Epicrius corniger* Berlese (1891) to be a synonym of *Sejus viduus* C. L. Koch. According to our generic concept *Cheiroseius*, *Episeius* and *Episeiella* are synonymous with *Sejus*.

The present revision of the Platyseiinae is based on material in the Collections of the British Museum (Natural History). The major collections were made by the late A. H. G. Alston (Indonesia), P. F. Bellinger (Jamaica), Miss T. Clay (Sikkim), G. Owen Evans (Uganda), K. H. Hyatt (Nepal), P. Wygodzynsky (Argentina) and M. E. Bacchus, P. N. Lawrence and J. T. Salmon (British Isles). The type material, unless otherwise stated, is deposited in the British Museum (Natural History).

EXTERNAL MORPHOLOGY

Gnathosoma

The chelicerae are chelate-dentate in all postembryonic developmental stages and show a marked uniformity in shape and dentition throughout the subfamily. The

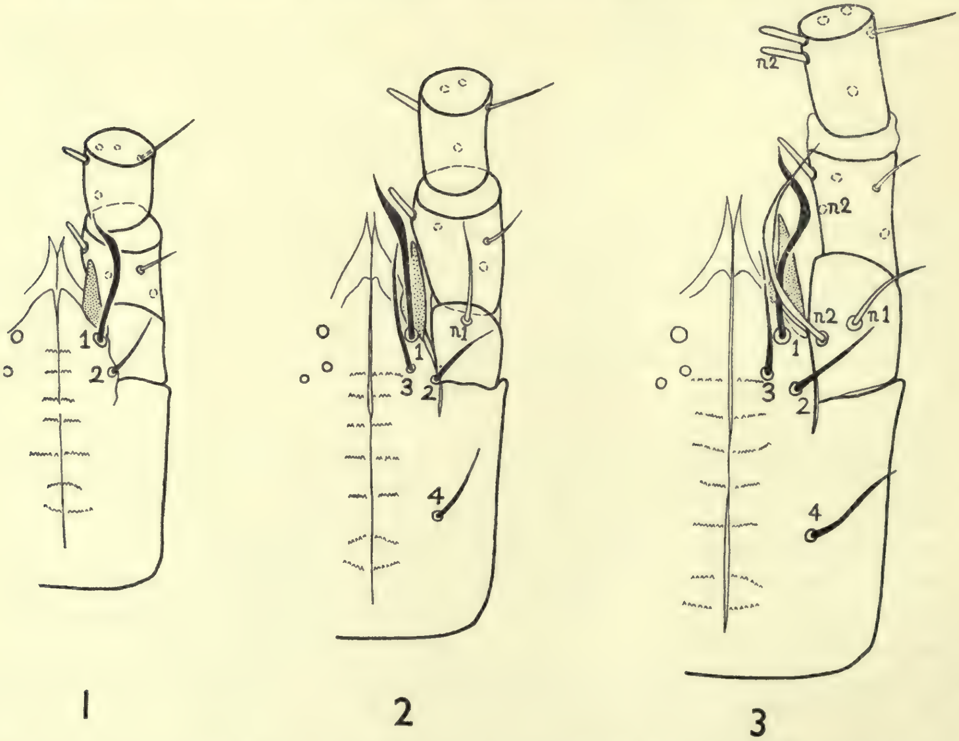
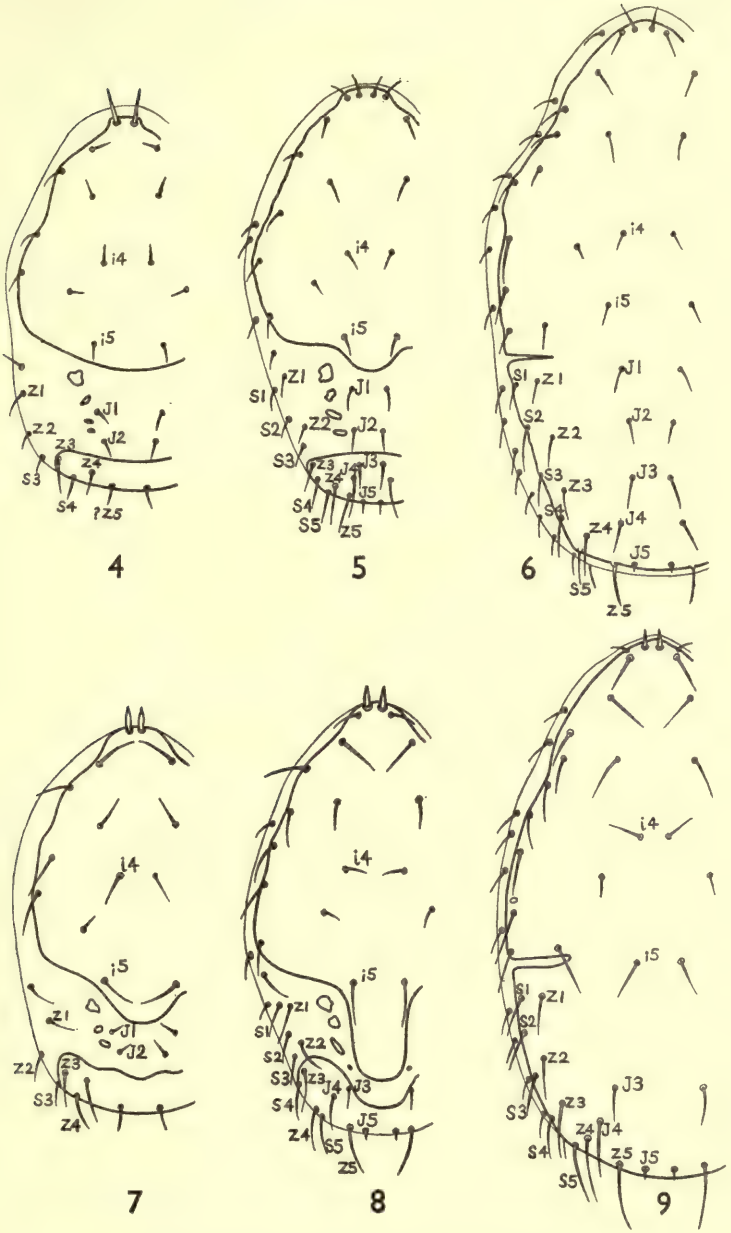


Fig. 1–3. Chaetotaxy of the venter of the gnathosoma and palptrochanter, femur and genu in the larva (1), protonymph (2), and deutonymph (3) of *Plesiosejus italicus* (Berlese).

1, rostral setae ; 2, external posterior rostral setae ; 3, internal posterior rostral setae ; 4, capitular setae ; n2, setae appearing in the deutonymph.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FIGS. 4–9. *Sejus necorniger* (Oudemans), dorsum of larva (4), protonymph (5), and deutonymph (6).

Plesiosejus italicus (Berlese), dorsum of larva (7), protonymph (8), and deutonymph (9).

spermatophoral process on the movable digit in the male shows considerable interspecific variation in form (e.g. Text-figs. 33 and 41) and appears to be a useful taxonomic character. In all stages the processes from the arthrodial membrane at the base of the movable digit are simple and setiform.

The postembryonic development of the chaetotaxy of the venter of the gnathosoma and of the three basal movable segments of the pedipalp is typically parasitoid (Text-figs. 1–3). The rostral setae (1) in the immature stages and in the adults are long and usually whip-like as are the internal palptrochanter setae which appear in the deutonymph. (This characteristic structure of these two pairs of setae is a useful character for separating the platyseiines from the closely related aceosejines). The corniculi are simple and the specialized seta at the inner basal angle of the palptarsus is two pronged. With the exception of *Sejus clayi* sp. nov., the tectum is basically tridentate with the processes subequal in length and inconspicuously divided distally (Text-figs. 28, 32 and 76). In *S. clayi* the median process is extremely long and Y-shaped with the lateral processes relatively shorter (Text-fig. 117).

Idiosoma

The idiosoma is usually elongate-oval in outline although in *Platyseius* it may be subcircular.

Dorsum : the dorsum of the larva has two weakly sclerotized shields. In *Sejus* and *Plesiosejus* the anterior shield bears nine pairs of setae and the pygidial four pairs[1] (Text-figs. 4 and 7). The striated cuticle between these sclerotized areas carries two pairs of J setae (J1 and J2), three pairs of Z setae (Z1–Z3) and one pair of S setae (? S3). Three or more platelets are also present on the cuticle. We have seen three main types of protonymph which chiefly differ in the chaetotaxy of the posterior half of the dorsum. All have an anterior shield with eleven or twelve pairs of setae and a pygidial shield. In the *Sejus*-type (Text-fig. 5) there are five pairs of setae in the J series ; J1 and J2 being situated on the cuticle between the anterior and pygidial shields. The protonymphs of both *Platyseius* and *Plesioseius*, on the other hand show a deficiency in the chaetotaxy of the J series. The former have only two pairs in the J series (J4 and J5) and the latter three pairs (J3–J5). There are no setae of the J series present on the cuticle between the anterior and pygidial shields in these genera (Text-fig. 8). All the deutonymphs we have examined have a laterally incised dorsal shield which almost entirely covers the dorsum of the mite. The chaetotaxy of the " anterior dorsal shield " (the region anterior to the incisions) is relatively constant but the number of setae on the " posterior shield " which is largely determined in the protonymph shows considerable variation. Four types may be readily recognized :

1. *Sejus*-type : J, Z and S series each with five pairs of setae (Text-fig. 6).

---

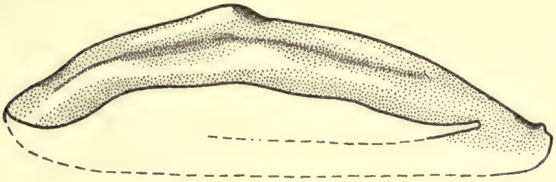
[1] The system of nomenclature for the dorsal chaetotaxy follows that proposed by Sellnick (1944) and added to by Hirschmann (1957). The latter author has used one system of nomenclature throughout the suborder and by so doing has attempted to homologize setae in widely differing groups. This may be possible in the larval stage but becomes increasingly difficult and purely subjective in subsequent developmental stages because of the increased number of setae, especially in those forms exhibiting hypertrichy.

2. *Zerconopsis*-type : J and Z series each with five pairs, S series with four pairs.

3. *Platyseius*-type : J series with two pairs (J4 and J5), Z and S series each with five pairs.

4. *Plesiosejus*-type : J series with three pairs (J3–J5), Z and S series each with five pairs (Text-fig. 9).

The dorsal shield in the adults is entire except in *S. clayi*, *Zerconopsis labradorensis* sp. nov. and *Zerconopsis muestari* (Schweizer) which retain the deutonymphal incisions and *Sejus ornatus* sp. nov. which has wide incisions between S2 and S3 (Text-fig. 168). The chaetotaxy of the "posterior dorsal shield" is essentially the same as in the deutonymph so that the above four groups may also be recognized in the adult. The surface of the shield is invariably reticulated and the majority of the species have a median longitudinal ridge (Text-figs. 10 and 11). The position of the highest point along this ridge varies throughout the group. It is usually located in the region of setae I4–J2 but in some species it may appear as a distinct tubercle between J4 and J5. The extreme attenuation of the posterior margin of the anterior shield in the protonymph of *Plesiosejus italicus* (Berl.) may be due to the development of the median ridge (cf. Text-figs. 8 and 36).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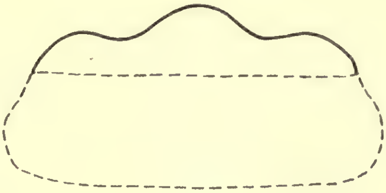
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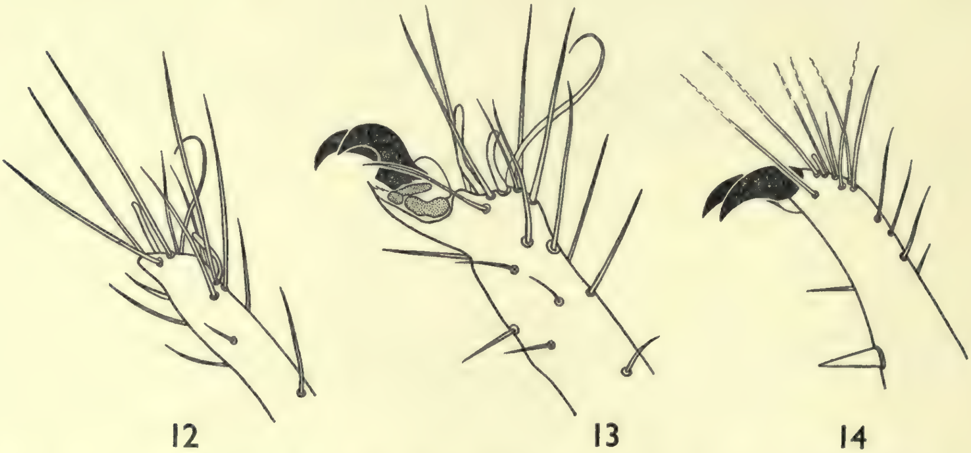
FIGS. 10–11. Dorsal shield of *Plesiosejus italicus* (Berlese). Fig. 10, lateral view. Fig. 11, transverse section.

Venter : The tritosternum is well developed in all stages and in the adult comprises a long slender base and a pair of strongly pilose laciniae. Pre-endopodal shields may be present in some species.

The development of the chaetotaxy of the intercoxal region is normal ; the larva having three pairs (homologous with sternal setae I–III in the adult), the protonymph four pairs (homologous with sternal setae I–III and the genital setae in the adult) and the deutonymph five pairs (the extra setae appearing at this stage being homologous with the metasternals in the adult). The female has a strongly sclerotized sternal shield bearing three pairs of setae and the metasternals are normally situated on discrete platelets.

The genital shield is wedge shaped and except in *S. clayi* and certain species of *Zerconopsis* has a pair of setae. A sterniti-genital shield is always present in the male although it may show various degrees of fusion with the ventral shield. The genital orifice in this sex is located near the anterior margin of the sterniti-genital. The larva has an anal shield usually with a seta on each anal valve in addition to the normal three setae present on the shield. There is a tendency for increased sclerotization of the anal region in subsequent developmental stages so that the protonymph and the deutonymph may have a ventri-anal shield (an anal shield with usually one pair of preanals). All the females of the platyseiines we have examined have a ventri-anal shield with from one to four pairs of pre-anals. Members of the genus *Platyseius* in addition have two or more pairs of setae situated in the posterior half of the shield (Text-fig. 23). The ventri-anal shield in the male shows varying degrees of fusion with the sterniti-genital shield and with the dorsal shield (Text-figs. 19 and 31).



FIGS. 12–14. Tarsi of leg I showing development of ambulacra. Fig. 12, *Sejus viduus* C. L. Koch. Fig. 13, *Sejus laelaptoides* (Berlese). Fig. 14, *Sejus unguiculatus* (Berlese).

The larva lacks stigmata and peritremes but the protonymph has a pair of stigmata located ventro-laterally between coxae III and IV and short peritremes. In the deutonymph, the peritremes are well developed and extend beyond the anterior margin of coxae I. The peritrematal shields at this stage, however, are weak and inconspicuous. The adults have large peritrematal shields ; these are invariably fused with the expodals and extend posterior to coxae IV (Text-fig. 16). Many species have a strong poststigmatic prolongation of the peritreme.

Legs : All the legs are usually long and slender. The structures of taxonomic importance are the form of the ambulacrum and the chaetotaxy of tarsi II–IV. The ambulacrum of leg I shows varying degrees of development. In a few species it is lacking (Text-fig. 12) but generally it comprises a lobate pulvillus and two claws. The claws may be minute or relatively large and conspicuous (Text-fig. 13). A short pretarsus is usually present ; a notable exception being *Sejus unguiculatus* (Berl.) in which the large claws on tarsus I are sessile (Text-fig. 14). The ambulacra of legs II–IV are well developed and each consists of a pair of claws and a lobate pulvillus. In the majority of the platyseiines, the median and lateral lobes of the pulvilli are slender and markedly acute—a probable adaptation for movement over a moist substratum. Tarsi II and III and usually IV have a pair of characteristic lanceolate setae (Text-fig. 18). Leg II in the male is never crassate or armed with spurs.

CLASSIFICATION

The characters previously used in separating the genera of the Platyseiinae, e.g. the outline of the idiosoma, the presence or absence of an ambulacrum on tarsus I and the form of the peritreme, are undoubtedly of some value in the practical classification of the subfamily but have no phylogenetic basis. We have concluded from our investigations of the external morphology of the group that the chaetotaxy and form of the dorsal shield in the adult and immature stages afford the most satisfactory characters for a natural classification. It is interesting to note that the variation in the form and in the chaetotaxy of the dorsal shield already noted for the Aceosejinae (Evans, 1958) is also evident in the Platyseiinae. Thus, there is a tendency towards the reduction in the number of the J and S setae on the " posterior dorsal shield " and towards the retention of the deutonymphal incisions. Our generic concept has as its basis the chaetotaxy of the " posterior dorsal shield " which has been discussed above.

Subfamily PLATYSEIINAE

Platyseiinae Evans, G. O., (1957), *J. Linn. Soc. Lond.* (*Zool.*), **43** : 244.

Aceosejids with the rostral and internal palptrochanter setae long and usually whip-like. Tarsi II and III with a pair of long lanceolate setae about the middle of the segment (Text-fig. 18). Dorsal shield in the adults entire, rarely with lateral incisions. " Posterior dorsal shield " normally with fifteen pairs of setae ; when fewer setae are present the J series or S series comprises less than five pairs. Females with sternal shield bearing three pairs of setae, a wedge-shaped genital shield with or without a pair of setae and a ventri-anal shield with one or more pairs of preanals. Male with sterniti-genital and ventri-anal shields, the latter often being partially fused with the dorsal shield. Both sexes with or without poststigmatic prolongation of the peritreme. Chelicerae chelate-dentate in both sexes ; movable digit with spermatophoral process in the male. Tectum basically three pronged. All legs usually slender ; leg I with or without ambulacrum, legs II–IV with pulvilli (often acutely lobate) and two claws. Leg II unarmed in the male.

KEY TO GENERA—ADULTS

1. " Posterior dorsal shield " with 5 pairs of setae in the J series (Text-fig. 53) . . 2
—" Posterior dorsal shield " with only 2 or 3 pairs of setae in the J series (Text-figs. 15 and 36) 3

2. " Posterior dorsal shield " with 5 pairs of setae in the S series (Text-fig. 53) ; dorsum never with paddle-like setae ; peritreme often with a strong poststigmatic process (Text-fig. 54) ; median lobes of the pulvilli of ambulacra II–IV usually acuminate (Text-fig. 58) . . . . *Sejus* C. L. Koch (p. 49)
   —" Posterior dorsal shield " with 4 pairs of setae in the S series, ? S2 situated on the lateral integument (Text-fig. 179) ; dorsal shield with three or more pairs of paddle-like setae, remainder of dorsal setae simple (Text-fig. 184) ; peritreme without poststigmatic prolongation ; median lobes of the pulvilli of legs II–IV rounded apically (Text-fig. 202) . . . . . . *Zerconopsis* Hull (p. 91)
3. Both sexes with three pairs of setae in the J series (Text-fig. 36) ; idiosoma elongate-oval in outline ; ventri-anal shield in the female with 3 or 4 pairs of setae in addition to the paranal and postanal setae . . . *Plesiosejus* gen. nov. (p. 42)
   —Both sexes with only 2 pairs of setae in the J series (J4 and J5) ; idiosoma usually subcircular in outline (Text-fig. 15) ; ventri-anal shield in the female with 5 or 6 pairs of setae in addition to paranal and postanal setae . *Platyseius* Berlese (p. 34)

Genus ***PLATYSEIUS*** Berlese

Platyseius Berlese, A., (1916). *Redia*, **12** : 42.

Platyseiine mites with the idiosoma usually subcircular in outline. Dorsal shield entire : " posterior dorsal shield " with J series comprising two pairs of setae (J4 and J5). Dorsal setae, with the exception of J5 in some species, long and simple. Sternal shield in the female with three pairs of setae ; metasternals situated on small plates. Genital shield wedge-shaped and with a pair of setae. Ventri-anal shield large and bearing 13 or 15 setae. Poststigmatic process of peritreme and peritrematal shield well developed and extending posterior to coxa IV. Male with sterniti-genital and ventri-anal shield, and ventri-anal shield showing varying degrees of fusion with the dorsal shield. Chaetotaxy of gnathosoma normal. Chelicerae chelate-dentate ; movable digit with spermatophoral process in the male. Tectum basically trispinate. All legs with ambulacra ; pulvilli of ambulacra II–IV acuminate.

Type species ***Lasioseius*** (***Platyseius***) ***capillatus*** Berlese, 1916

(=***Hypoaspis subglabra*** Oudemans, 1902)

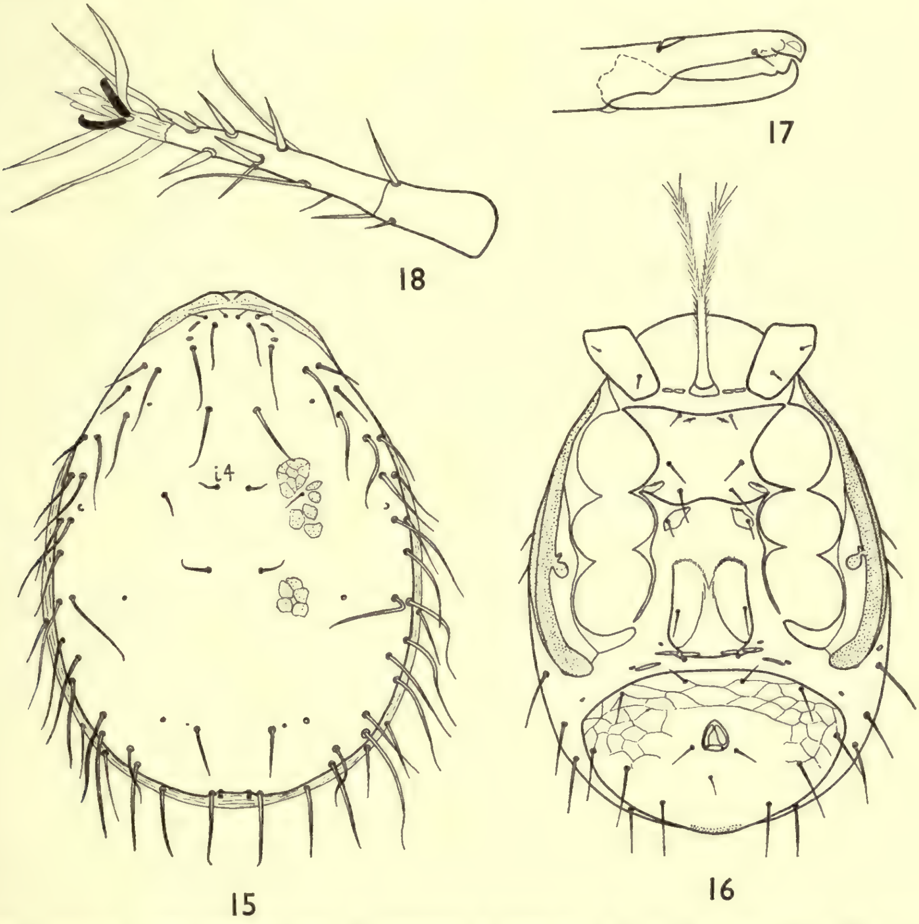
KEY TO SPECIES—FEMALES

1. Setae i5 shorter than J4 (Text-fig. 15) ; ventri-anal shield with 13 setae ; pre-endopodal shields present. Europe . . . *P. subglaber* (Oudms.) (p. 35)
   —Setae i5 at least twice the length of J4 (Text-fig. 22) 2
2. Ventri-anal shield with 15 setae (Text-fig. 27) ; pre-endopodal shields absent. Jamaica . . . . *P. jamaicensis* sp. nov. (p. 39)
   —Ventri-anal shield with 13 pairs of setae (Text-fig. 23) ; pre-endopodal shields present 3
3. Setae on ventri-anal shield simple (Text-fig. 23) ; setae J5 thorn-like, smooth. Indonesia . . . . *P. mollicomus* Berl. (p. 37)
   —Two pairs of setae on the posterior half of the ventri-anal shield stout, spinose (Text-fig. 35) ; setae J5 short, brush-like. East Africa *P. spinosus* sp. nov. (p. 41)

Platyseius subglaber (Oudemans), 1903

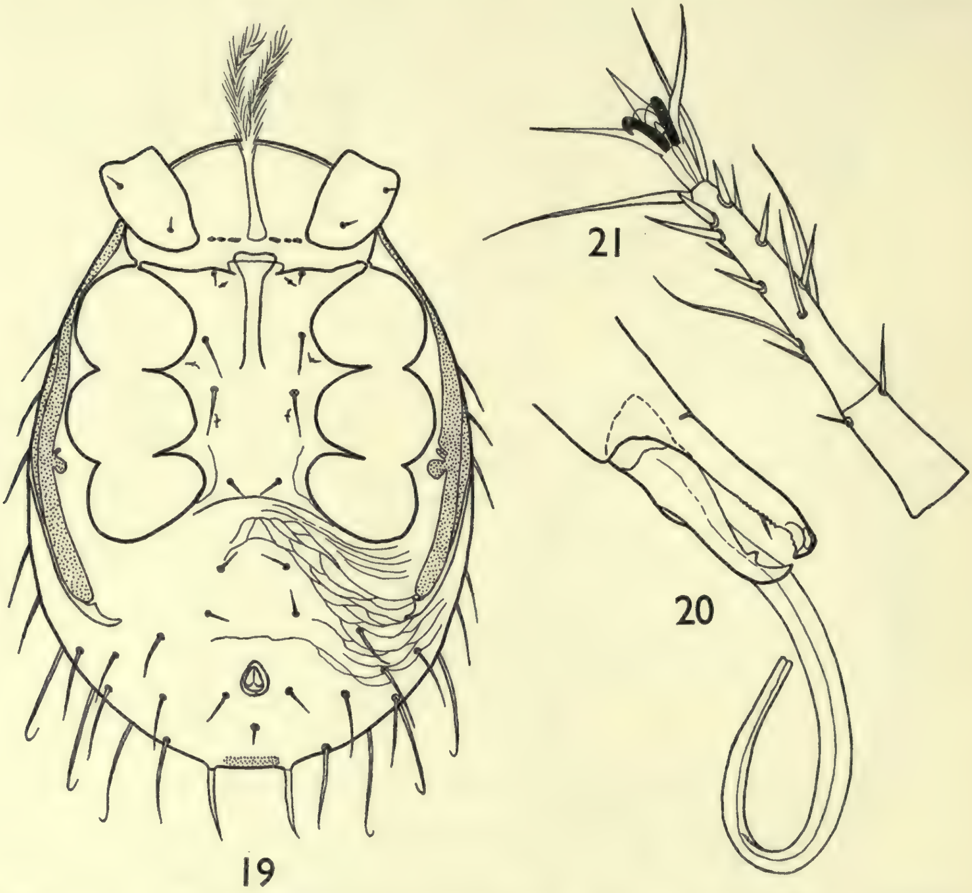
Hypoaspis subglabra Oudemans, A. C., (1903). *Ent. Ber.*, **1** : 87 ; *Abh. nat. Ver. Bremen*, **18** : 88.
Lasioseius (*Platyseius*) *capillatus* Berlese, A., (1916). *Redia*, **12** : 43, syn. nov.
Lasioseius (*Platyseius*) *subglaber*, Halbert, J. N., (1923). *J. Linn. Soc. Lond.* (*Zool.*), **35** : 373.
Lasioseius (?) *listrophorus* Schweizer, J., (1924). *Arch für Hydrobiol.*, **15** : 131.

FEMALE. Dorsal shield (560 μ × 361–477 μ) broadly oval; ornamentation restricted to a number of small punctate areas. "Anterior dorsal shield" with nineteen pairs of simple setae; verticals very fine and short (Text-fig. 15). "Posterior dorsal shield" with twelve pairs of setae; J1–J3 being absent. Setae J5 short, palmate. The distribution and relative lengths of the setae on the dorsal shield and lateral interscutal membrane are shown in the figure.



FIGS. 15–18. *Platyseius subglaber* (Oudemans), female. Fig. 15, dorsum. Fig. 16, venter. Fig. 17, chelicera. Fig. 18, tarsus II.

Tritosternum large with a pair of strongly-pilose laciniae, and flanked at its base by two pairs of pre-endopodal shields. Sternal shield smooth and with three pairs of simple setae (Text-fig. 16). Genital shield wedge shaped and with a pair of setae. Ventri-anal shield wider than long (202–215 μ long × 280–360 μ wide), reticulated in its anterior half and bearing thirteen setae. Six small sclerotized plates are situated between the genital and ventri-anal shields. Stigma situated between coxae III and IV; peritreme extending posterior to the stigma; peritrematal shield strongly developed. Metapodal shields apparently fused with the peritrematal shields.



Figs. 19–21. *Platyseius subglaber* (Oudemans), male. Fig. 19, venter. Fig. 20, chelicera. Fig. 21, tarsus II.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum three-pronged and typical of the genus. Dentition of chelicerae as in Text-fig. 17.

Leg I (670–772 μ long) with the tarsus (160–177 μ) considerably longer than the tibia (126–140 μ). Setae on tibia and tarsus fine, those on remaining segments stouter. Tarsi II–IV with a pair of long lanceolate setae. Ambulacrum of tarsus I short and claws small. Pulvilli of ambulacra II–IV produced into three long acuminate lobes (Text-fig. 18).

MALE. Dorsal shield (425–467 μ × 340–371 μ) is similar to that of the female. " Anterior dorsal shield " with nineteen pairs of simple setae and " posterior dorsal shield " with twelve pairs of setae.

The tritosternum is flanked at its base by two or three pairs of small pre-endopodal shields. The remainder of the chaetotaxy and sclerotization of the venter is shown in Text-fig. 19.

The gnathosoma and tectum are similar to those of the female. The spermatophoral process is about three times as long as the movable digit of the chelicera. The dentition of the chelicera, and the spermatophoral process are shown in Text-fig. 20.

Leg I (602–682 μ long) has the tarsus (147–177 μ) considerably longer than the tibia (114–126 μ). The chaetotaxy of the legs is as in the female. The ambulacra of tarsi II–IV are provided with lanceolate pulvilli (Text-fig. 21).

DISTRIBUTION. This species is widely distributed in western Europe. In Great Britain we have examined specimens from Cumber Park, Nottinghamshire (coll. G. O. E., April, 1955), Dungeness, Kent (coll. D. A. Chant, July, 1955), Box Hill, Surrey (coll. E. Duffey, 30.vi.1951), and St. Agnes, Isles of Scilly (coll. K. H. H., September, 1957).

Platyseius mollicomus Berlese, 1916

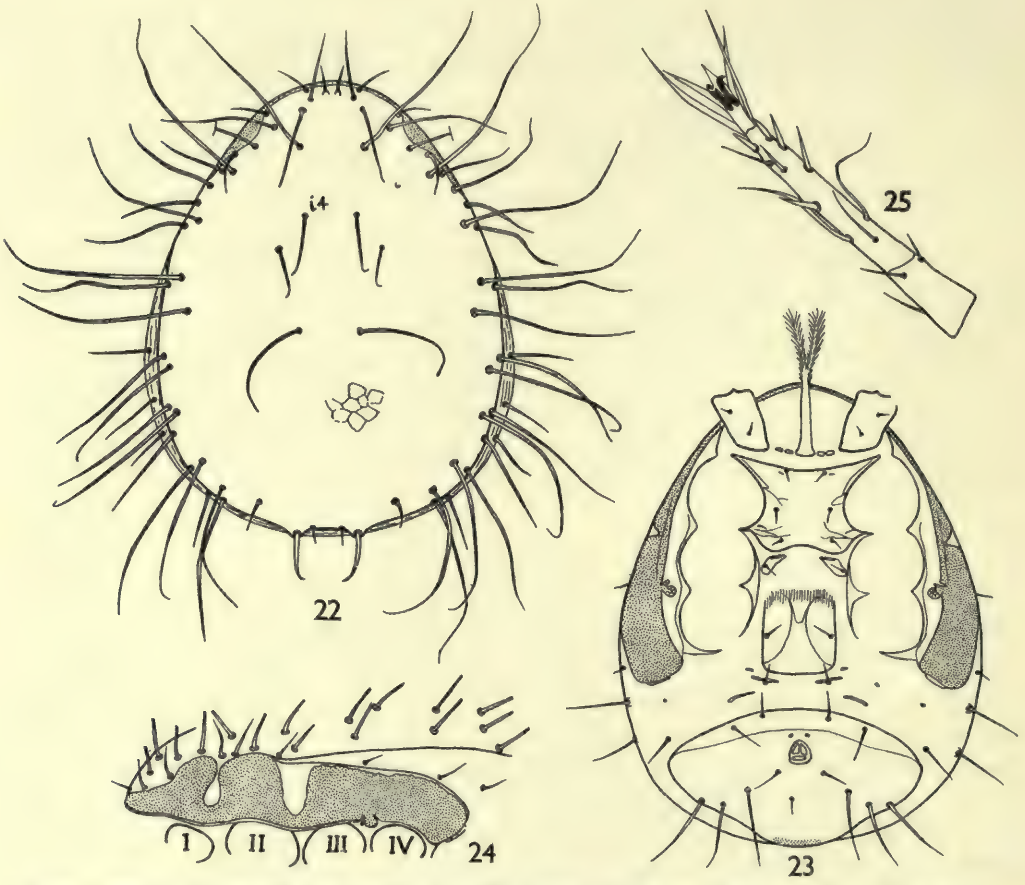
Lasioseius (*Platyseius*) *mollicomus* Berlese, A., (1916). *Redia*, **12** : 43.
Platyseius mollicomus, Vitzthum, H. G., (1931). *Arch. für Hydrobiol.*, Suppl., **9** : 70, figs.

FEMALE. Dorsal shield (570–580 μ × 467–480 μ) broadly oval in outline; ornamentation restricted to a number of faint reticulated areas. " Anterior dorsal shield " with twenty-one pairs of simple setae (Text-fig. 22). " Posterior dorsal shield " with twelve pairs of simple setae; J1–J3 being absent. Setae J5 are short and simple. The distribution and relative lengths of the setae on the dorsal shield are shown in the Text-fig.

Tritosternum large with a pair of strongly pilose laciniae, and flanked at its base by two pairs of pre-endopodal shields. Sternal shield with three pairs of simple setae and faintly reticulated (Text-fig. 23). Genital shield slightly convex posteriorly and with a pair of setae. Ventri-anal shield wider than long (177 μ long × 318 μ wide) with a transverse line anteriorly, and bearing thirteen setae. Four small sclerotized plates are situated between the genital and ventri-anal shields. Stigma situated between coxae III and IV. Peritreme broad, occupying most of the peritrematal shield, and with two deep indentations (Text-fig. 24), and extending posterior to the stigma. Metapodal shields fused with the peritrematal shields.

Venter of gnathosoma with rostral and internal palptrochanter setae long and whip-like. All setae on pedipalp simple. Tectum three-pronged and typical of the genus. The chelicerae are typical.

Leg I (700–760 μ long) with the tarsus (202 μ) longer than the tibia (126 μ). Setae on tarsus fine, those on remaining segments stouter. Tarsi II–IV with a pair of long lanceolate setae. Ambulacrum of tarsus I fairly short and claws small. Pulvilli of ambulacra II–IV produced into three acuminate lobes (Text-fig. 25).



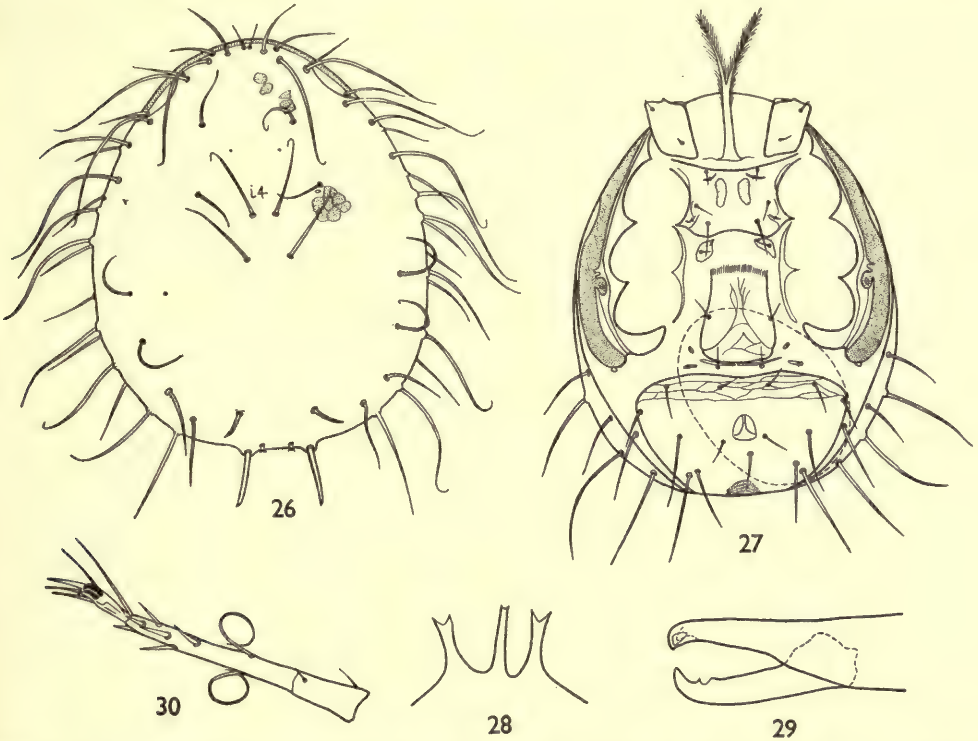
Figs. 22–25. *Platyseius mollicomus* Berlese, female. Fig. 22, dorsum. Fig. 23, venter. Fig. 24, peritrematal shield. Fig. 25, tarsus II.

Male. This sex (415 μ × 340 μ) is described by Vitzthum (1931) who also gives a figure of the chelicera.

Distribution. Berlese (1916) based his description on material collected in Java by Cl. Jacobson. Vitzthum (1931) examined specimens (male, female and deutonymph) from Tjibodas, Java (Indonesia). The Museum Collections contain a female and a deutonymph collected by A. H. G. Alston in decaying leaves and fruit, Bogor, Indonesia (1956.2.27.6) ; and a single female collected by G. Owen Evans in grassland nine miles north-east of Bundibugyo, Ruwenzori, Uganda, 24.viii.1952 (1959.1.20.1).

Platyseius jamaicensis sp. nov.

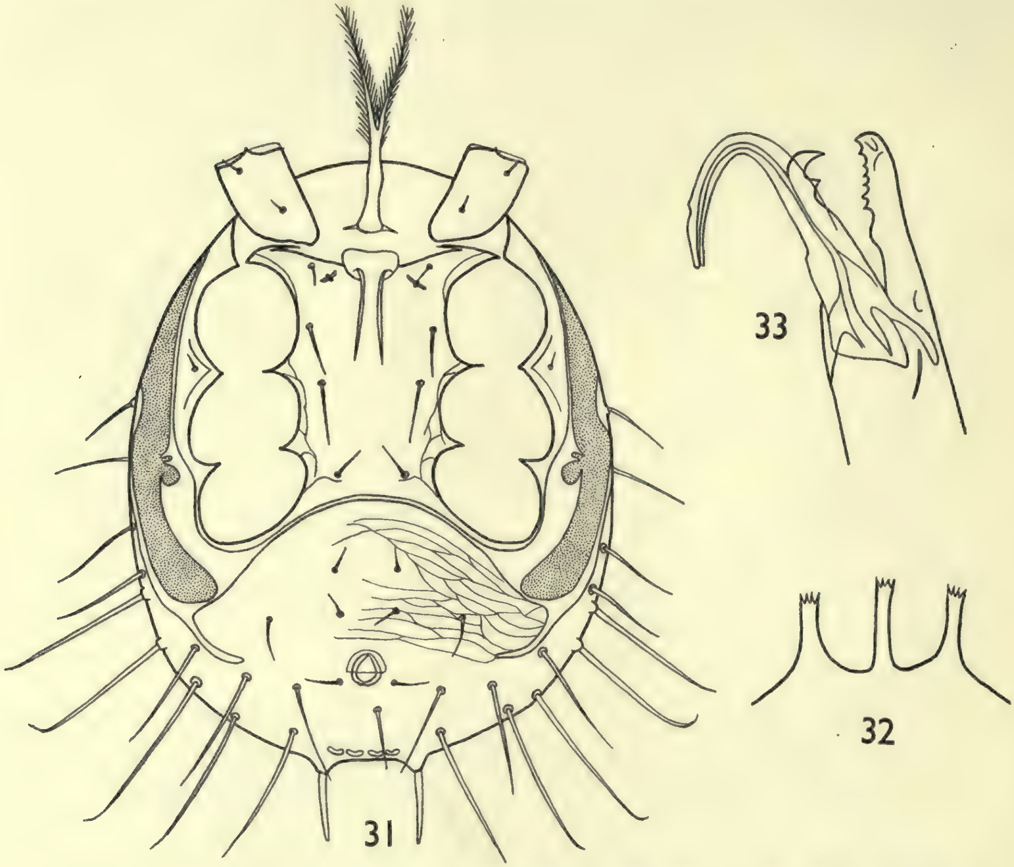
FEMALE. Dorsal shield (498 μ × 392–402 μ) broadly oval in outline ; ornamentation restricted to a number of small punctate areas. " Anterior dorsal shield " with twenty pairs of simple setae of which the verticals are the shortest (Text-fig. 26). " Posterior dorsal shield " with thirteen pairs of setae ; J1–J3 being absent. Setae J5 short, palmate and inconspicuous. J4 and Z5 are stout. The distribution and relative lengths of the setae on the dorsal shield are shown in the Text-fig.



FIGS. 26–30 *Platyseius jamaicensis* sp. nov., female. Fig. 26, dorsum. Fig. 27, venter. Fig. 28, tectum. Fig. 29, chelicera. Fig. 30, tarsus II.

Tritosternum large with a pair of strongly-pilose laciniae. Sternal shield with a pair of longitudinal elongate punctate areas and three pairs of simple setae (Text-fig. 27). Genital shield convex posteriorly and finely reticulated, with a pair of setae. Ventri-anal shield wider than long (152 μ long × 253–273 μ wide), reticulated anteriorly and bearing fifteen setae. Four small sclerotized plates are situated between the genital and ventri-anal shields. Stigma situated between coxae III and IV, peritreme extending posterior to the stigma; peritrematal shield strongly developed. Metapodal shields apparently fused with the peritrematal shields.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum (Text-fig. 28) three-pronged and typical of the genus. Dentition of chelicera as in Text-fig. 29.



FIGS. 31–33. *Platyseius jamaicensis* sp. nov., male. Fig. 31, venter. Fig. 32, tectum. Fig. 33, chelicera.

Leg I (about 770 μ long) with the tarsus (177 μ) longer than the tibia (157 μ). Setae on tibia and tarsus very fine: those on remaining segments stouter. Tarsi II–IV with a pair of long lanceolate setae. Ambulacrum of tarsus I short and the claws small. Pulvilli of ambulacra II–IV produced into three acuminate lobes (Text-fig. 30).

Male. Dorsal shield (498 μ × 310 μ) similar to that of the female. The tritosternum is of the same form as in the female. The chaetotaxy and sclerotization of the venter are shown in Text-fig. 31.

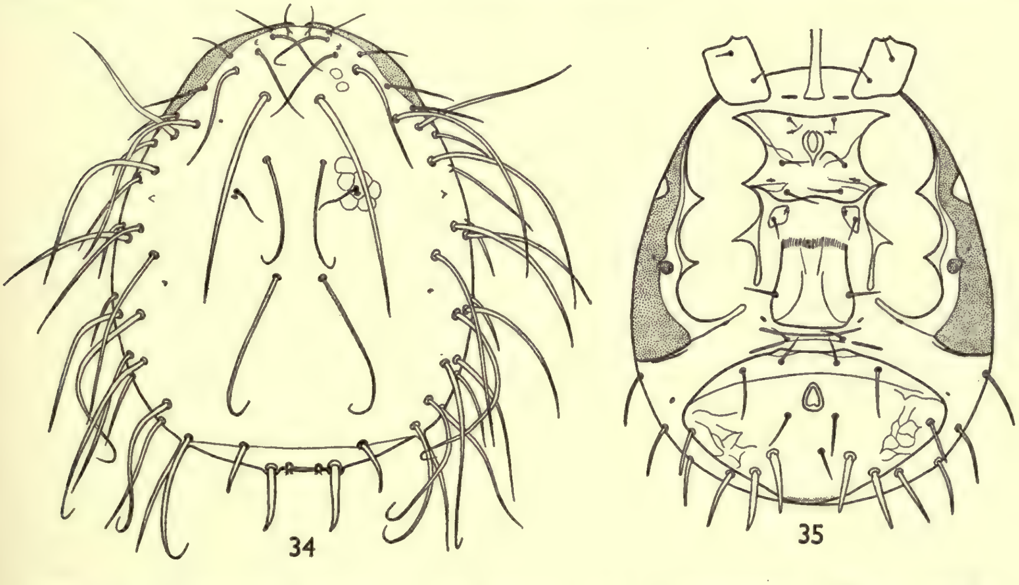
The gnathosoma is similar to that of the female, and the tectum is shown in Text-fig. 32. The spermatophoral process is about twice as long as the movable digit of the chelicera (Text-fig. 33).

Leg I (c. 680 μ) with the tarsus and tibia each 152 μ. The chaetotaxy and ambulacra of the legs are as in the female.

Locality. Jamaica, B.W.I. The holotype female (1959.1.20.18) and one paratype from Fairy Glade, St. Andrew, in *Lycopodium*, 4,300 ft., 6.xii.1956; and the allotype male (1959.1.20.19) from St. Thomas, John Cove Mountains, in moss, 2,300 ft., 25.v.1956 collected by P. F. Bellinger. The paratype female has been returned to the collector.

Platyseius spinosus sp. nov.

Female. Dorsal shield (498 μ × 402 μ) broadly oval in outline; ornamentation restricted to a number of very faint reticulated areas. "Anterior dorsal shield" with twenty-one pairs of simple setae (Text-fig. 34). Posterior dorsal shield with thirteen pairs of simple setae; J1–J3 being absent. Setae J5 are short, palmate and inconspicuous. Z5 are stout. The distribution and relative lengths of the setae on the dorsal shield are shown in the Text-fig.



Figs. 34–35. *Platyseius spinosus* sp. nov., female. Fig. 34, dorsal shield. Fig. 35, venter.

Tritosternum large with a pair of strongly-pilose laciniae, and flanked at its base by one or two pairs of pre-endopodal shields. Sternal shield with three pairs of simple setae and with a characteristically-shaped central mark (Text-fig. 35). Genital shield slightly convex posteriorly and with a pair of setae. Ventri-anal shield wider than long (177 μ long × 298 μ wide) with a transverse line anteriorly and bearing thirteen setae of which two pairs are stout. A narrow sclerotized band and two narrow plates are situated between the genital and ventri-anal shields. Stigma situated between coxae III and IV, peritreme broad, occupying most of the peritrematal shield, with a deep indentation, and extending posterior to the stigma. Metapodal shields fused with the peritrematal shields.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum three-pronged and typical of the genus. The chelicerae are typical.

Leg I (707 μ long) with the tarsus (202 μ) longer than the tibia (126 μ). Setae on tarsus fine; those on remaining segments stouter. Tarsi II–IV with a pair of long lanceolate setae. Ambulacrum of tarsus I short and claws small. Pulvilli of ambulacra II–IV produced into three acuminate lobes.

MALE. Unknown.

LOCALITY. Ruwenzori, Uganda. A single female (1959.1.20.20), collected by G. Owen Evans, in grassland at 2,850 ft., 24.viii.1952, nine miles north-east of Bundibugyo.

Genus ***PLESIOSEJUS*** gen. nov.

Platyseiine mites with the "posterior dorsal shield" having only three pairs of setae in the J series (J1 and J2 absent). Z and J series each with five pairs. Lateral margins of the dorsal shield entire in the adult stages. Vertical setae present or absent. Sternal shield in the female with three pairs of simple setae; metasternals free. Genital shield wedge-shaped and bearing a pair of setae. Ventri-anal shield large with three or four pairs of setae in addition to the paranals and the postanal seta. Male with sterniti-genital and ventri-anal shields, the latter showing varying degrees of fusion with the podal-peritrematal and dorsal shields.

Type species ***Ameroseius italicus*** Berlese, 1905

KEY TO SPECIES—FEMALES

1. Without poststigmatic prolongation of peritreme (Text-fig. 50); majority of dorsal setae long, stout (Text-fig. 49); vertical setae well developed, directed anteriorly; ventri-anal shield with 9 setae. Jamaica . . . *P. horridus* sp. nov. (p. 48)
—With strong poststigmatic prolongation of peritreme extending posterior to coxa IV; dorsal setae considerably shorter (Text-fig. 36); vertical setae absent; ventri-anal shield with 11 setae 2
2. Dorsal shield with distinct "tubercle" posterior to J4 (Text-fig. 36). Europe *P. italicus* (Berlese), (p. 43)
—Dorsal shield without such "tubercle" (Text-fig. 42). *P. major* (Halbert), (p. 47)

Plesiosejus italicus (Berlese), comb. nov.

Ameroseius italicus Berlese, A., (1905). *Redia*, **2** : 234 ; (1906). *Ibid.*, **6** : tav. 19, Text-figs. 35, 35a.
Paraseius tenuipes Halbert, J. N. (1915). *Proc. R. Irish Acad.*, **39**ii : 78, syn. nov.
Lasioseius italicus Berlese, A., (1916). *Redia*, **12** : 34.
? *Lasioseius* (*Episeius*) *michaeli* Halbert, J. N., (1923). *J. Linn. Soc. Lond.* (*Zool.*), **35** : 373.
Episeius tenuipes, Schweizer, J., (1949). *Rés. Rech. sci. Parc Nat. Suisse, N.F.* **2** : 60.
E. tenuipes, Franz, H., (1943). *Denkschr. Akad. Wiss. Wien.*, **107** : 87.

FEMALE. Dorsal shield (550–651 μ long × 310–402 μ wide) oval; ornamentation comprising a reticulated pattern covering the whole shield (Text-fig. 36). " Anterior dorsal shield " with twenty pairs of simple setae ; verticals absent. " Posterior dorsal shield " with thirteen pairs of setae ; J1–J2 being absent ; J5 are finely pilose. A strong tubercle arising posterior to setae J3 denotes the highest point on the median ridge of the dorsal shield. The distribution and relative lengths of the setae and the structure of the dorsal shield are shown in the Text-fig.

Tritosternum well developed with pilose laciniae, and flanked at its base by one or two pairs of small pre-endopodal shields. Sternal shield with three pairs of simple setae and two oval areas antero-medially (Text-fig. 37). Genital shield convex posteriorly, and bearing one pair of setae. Ventri-anal shield considerably wider than long (177–202 μ long × 265–341 μ wide), reticulated and bearing eleven simple setae. Between the genital and ventri-anal shields lie six narrow sclerotized plates. Stigma between coxae III and IV and the peritreme extending posterior to coxa IV ; peritrematal shield strongly sclerotized. Metapodal shields free and transversely situated.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum three-pronged and typical of the genus. The dentition of the chelicera is shown in Text-fig. 38.

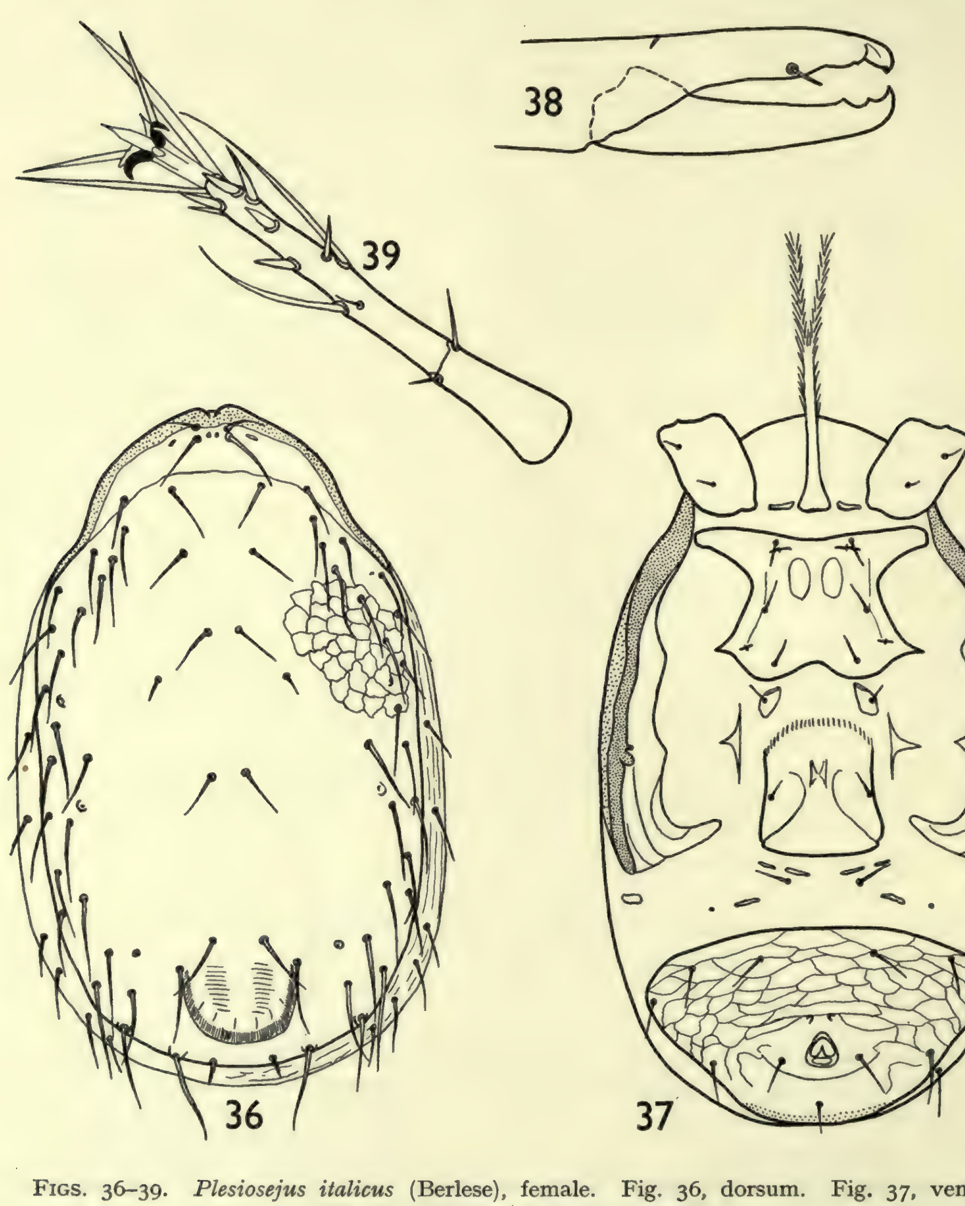
Leg I (639–726 μ long) with the tarsus (167–195 μ) longer than the tibia (113–129 μ). Setae on tarsus and tibia very fine ; those on remaining segments stouter ; ambulacra short and claws small. Tarsi II–IV with a pair of lanceolate setae ; pulvilli produced into three acuminate lobes (Text-fig. 39).

MALE. Dorsal shield (467–507 μ long × 279–310 μ wide) entirely reticulated as in the female. " Anterior dorsal shield " with nineteen pairs of simple setae, verticals absent. " Posterior dorsal shield " with thirteen pairs of setae ; J1–J3 absent ; J5 short and pilose. Postero-dorsal tubercle not so pronounced as in the female.

Tritosternum as in the female. The chaetotaxy and sclerotization of the venter are shown in Text-fig. 40. The gnathosoma and tectum are similar to those of the female. Spermatophoral process four times as long as the movable digit of the chelicera (Text-fig. 41).

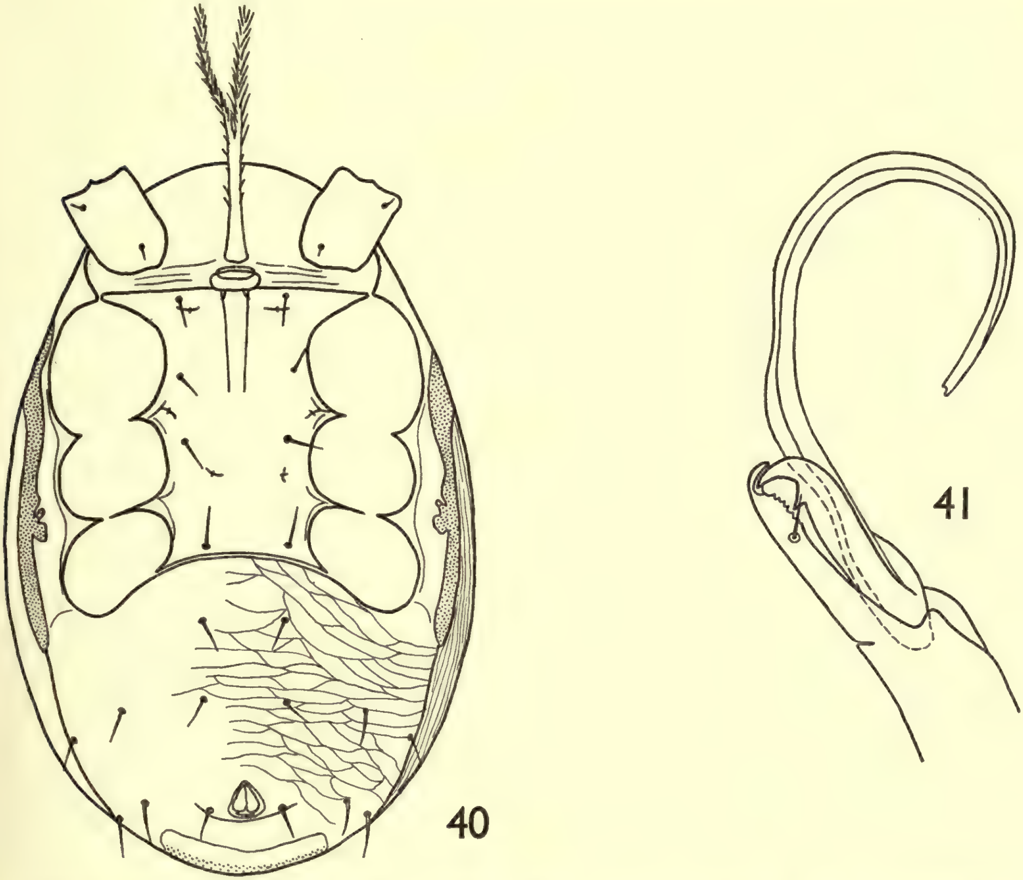
Leg I (534 μ long) with the tarsus (147–152 μ) longer than the tibia (96–106 μ). The chaetotaxy and ambulacra of the legs are similar to the female.

Distribution. Berlese's (1905 and 1916) descriptions of the male and female of *italicus* are based on specimens collected under dead rotting leaves on a marsh at Udine in northern Italy. Halbert (1915) described *P. tenuipes* from a single female " found amongst moss on a stone in a mountain stream at Glencree, County Dublin, May ". Schweizer (1949) records *tenuipes* from the Swiss National Park. We have

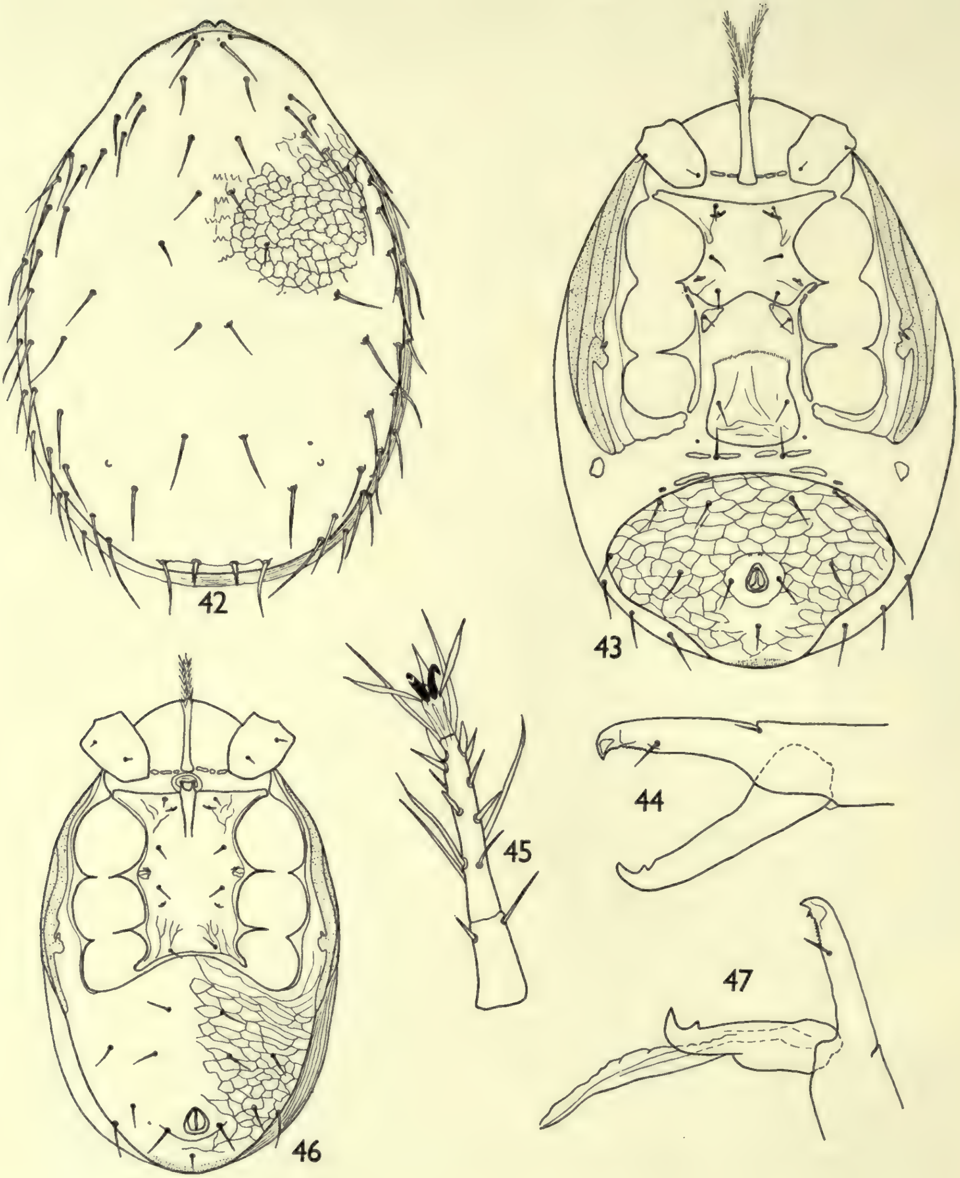


Figs. 36–39. *Plesiosejus italicus* (Berlese), female. Fig. 36, dorsum. Fig. 37, venter. Fig. 38. chelicera. Fig. 39, tarsus II

examined British specimens from the following localities: Thirlmere, Cumberland, 25.ix.1956, coll. P. N. Lawrence; Grasmere, Westmorland, 29.vi.1951, coll. J. T. Salmon; Blelham Tarn, Lancashire, 22.iii.1955, coll. R. J. Elliott; summit of Snowdon, Caernarvonshire, August, 1951, coll. E. Duffey; Minworth, Birmingham, 10.ix.1952, coll. T. G. Tomlinson; Swithland Wood and Anstey, Leicestershire, 19.iv.1958, coll. P. N. L.; Sea Houses, Northumberland, 1.x.1951, coll. J. T. Salmon; Oxted, Surrey, 20.i.1957, coll. P. N. L.; Leith Hill, Surrey, 6.vi.1951, coll. J. T. Salmon; Keston, Kent, 2.viii.1957, coll. P. N. L.; Dungeness, Kent, 8.vii.1955, coll. D. A. Chant; Avonmouth, Gloucestershire, 11.v.1957, coll. P. N. L.; Combe Martin, Devonshire, March and June, 1957, coll. P. N. L. and M. E. Bacchus; Porth Gwarra, Cornwall (A. D. Michael Coll.); The Burren, Co. Clare, 6.vi.1951, coll. E. A. J. Duffy.



Figs. 40–41. *Plesiosejus italicus* (Berlese), male. Fig. 40, venter. Fig. 41, chelicera.



FIGS. 42–47. *Plesiosejus major* (Halbert). Fig. 42, dorsum of female. Fig. 43, venter of female. Fig. 44, chelicera of female. Fig. 45, tarsus II of female. Fig. 46, venter of male. Fig. 47, chelicera of male.

Plesiosejus major (Halbert), comb. nov.

Lasioseius (*Episeius*) *major* Halbert, J. N., (1923). *J. Linn. Soc. Zool. Lond.* **35** : 373.
Lasioseius (*L.*) *tenuipes*, Schweizer, J., (1922). *Verh. Naturf. Ges. Basel*, **33** : 43.
Episeius major, Schweizer, J., (1949). *Rés. Rech. sci. Parc Nat. Suisse, N.F.* **2** : 61.

FEMALE. Dorsal shield (581–740 μ long × 371–488 μ wide) broadly oval in outline : ornamentation consisting of a dense reticulated pattern covering the whole of the shield (Text-fig. 42). " Anterior dorsal shield " with twenty pairs of simple setae. " Posterior dorsal shield " with thirteen pairs of setae ; J1–J2 being absent ; setae J5 are short and spiculate. The distribution and relative lengths of the dorsal setae are shown in the Text-fig.

Tritosternum well developed with pilose laciniae, and flanked at its base by two or three pairs of small pre-endopodal shields. Sternal shield with three pairs of simple setae (Text-fig. 43). Genital shield with one pair of setae and slightly convex posteriorly. Ventri-anal shield wider than long (203–253 μ long × 288–379 μ wide), strongly reticulated and bearing eleven simple setae. Six narrow sclerotized plates are situated transversely on the membrane between the genital and ventri-anal shields. Stigma situated between coxae III and IV with the peritreme extending posterior to coxa IV. Peritrematal shield strongly sclerotized. Metapodal shields free and obliquely situated.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whiplike. All setae on pedipalp simple. Tectum three-pronged and typical of the genus. The dentition of the chelicera is shown in Text-fig. 44.

Leg I (681–797 μ long) with the tarsus (147–177 μ) longer than the tibia (106–152 μ) ; pulvillus short, claws small. Setae on tarsus and tibia very fine ; those on remaining segments stouter. Tarsi II–IV with a pair of lanceolate setae ; pulvilli produced into three acuminate lobes (Text-fig. 45).

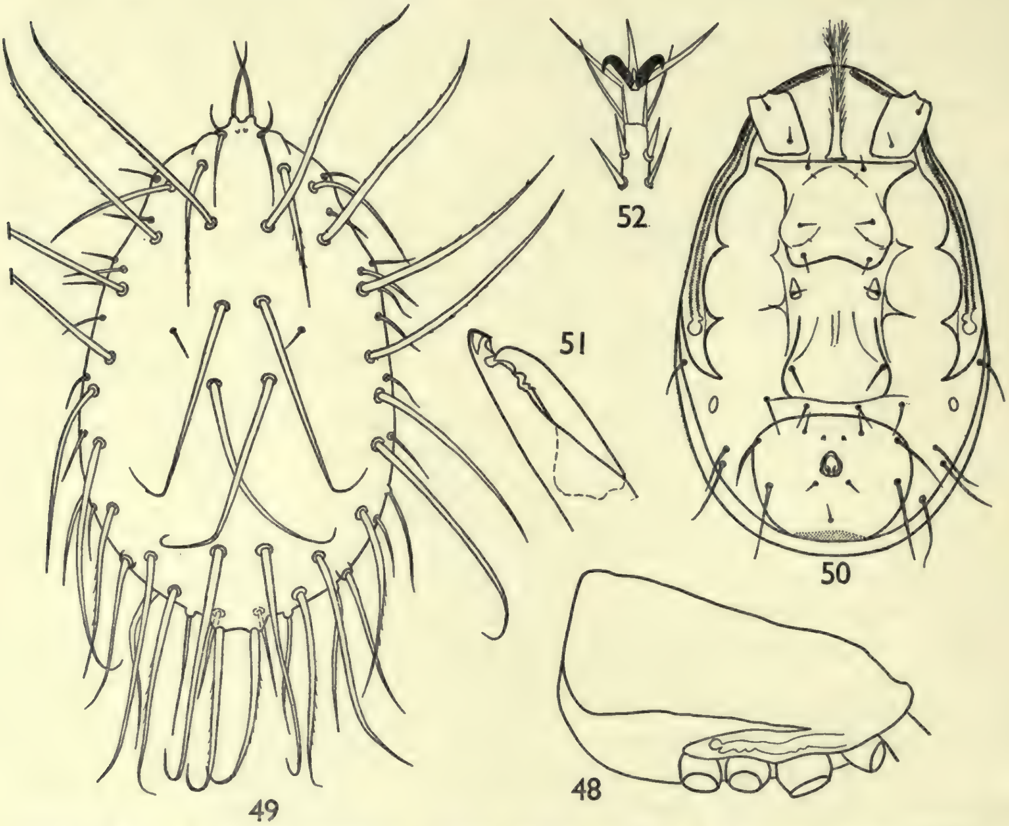
MALE. Dorsal shield (550 μ long × 340 μ wide) of the same form and chaetotaxy as the female. The structure and chaetotaxy of the venter are shown in Text-fig. 46. The gnathosoma and tectum are similar to those of the female. The spermatophoral process is twice as long as the movable digit of the chelicera (Text-fig. 47).

Leg I (670 μ long) with the tarsus (165 μ) longer than the tibia (126 μ). The legs are similar to those of the female.

DISTRIBUTION. Halbert's (1923) description of males and females of this species is based on specimens found in moss in streams at Kilmashogue and Glencullen in Ireland, and at Mill Bay, Land's End, England. Schweizer (1922) described what he considered to be males of *Lasioseius tenuipes* (Halbert) from Basel, Switzerland, but his figures show clearly that his specimens are *Plesiosejus major* (Halbert). In 1949 the same author recorded *major* from the Swiss National Park. We have examined specimens collected by the River Tolka, Glasnevin, Co. Dublin (Halbert Collection), and from the following localities : Oxted, Surrey, 20.i.1957, coll. P. N. Lawrence ; Cumber Park, Nottinghamshire, April, 1955, coll. G. O. E. ; Markfield and Anstey, Leicestershire, 19.iv.1958, coll. P. N. L.; Blea Tarn, Westmorland, 27.ix.1956, coll. P. N. L.; and Chorley, Lancashire, 21.xi.1940, coll. Water Pollution Research Laboratory. All these British specimens were collected from wet habitats (mosses, etc.).

Plesiosejus horridus sp. nov.

Female. Dorsal shield (350 μ long × 218 μ wide) narrower in outline than in the other species of the genus, and is steeply elevated posteriorly (Text-fig. 48).



Figs. 48–52. *Plesiosejus horridus* sp. nov., female. Fig. 48, lateral view of dorsum. Fig. 49, dorsal shield. Fig. 50, venter. Fig. 51, chelicera. Fig. 52, tarsus II.

There is no noticeable ornamentation on the dorsal shield. "Anterior dorsal shield" with twenty pairs of setae. J1–J3 absent. Setae J5 are partly concealed by the postero-dorsal elevation of the dorsal shield which bears J4 at its apex (Text-fig. 49). The distribution and relative lengths of the dorsal setae are shown in the Text-fig.

Tritosternum well developed with pilose laciniae. Sternal shield with three pairs of short simple setae (Text-fig. 50). Genital shield flask shaped with a pair of setae. Ventri-anal shield slightly wider than long (93 μ long × 113 μ wide), with nine setae of which two lateral pairs are long. There appears to be a narrow sclerotized band between the genital and ventri-anal shields. Stigma between coxae III and IV, with the narrow, crenate peritreme not extending posterior to the stigma. Peritrematal shield extending to the posterior margin of coxa IV. Metapodal plates oval, free.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum three-pronged and typical of the genus. The dentition of the chelicera is shown in Text-fig. 51.

Leg I (370 μ long) with the tarsus (96 μ) one-and-a-half times as long as the tibia (63μ). Setae on tarsus very fine; those on remaining segments stouter. Tarsi II–IV with a pair of lanceolate setae. Tarsus I without claws. Pulvilli of tarsi II–IV produced into three acuminate lobes (Text-fig. 52). Leg IV 370 μ long with the tarsus 130 μ.

MALE. Unknown.

LOCALITY. Jamaica, B.W.I. The holotype female (1959.1.20.41) and two paratype females (1959.1.20.42) in damp leaf litter, St. Ann, Mt. Diablo, 2,200 ft., 3.vi.1956, collected by P. F. Bellinger. One paratype has been returned to the collector.

Genus *SEJUS* C. L. Koch

Sejus Koch, C. L., (1843)[1] *Übers. d. Arachnidensyst., Heft* **3** : 92.
Cheiroseius Berlese, A., (1916). *Redia,* **12** : 33.
Episeius Hull, J. E., (1918). *Trans. nat. Hist. Soc. Northumb.* (*n.s.*), **5** : 63.
Episeiella Willmann, C., (1938). *Ann. Hist. nat. Mus. Hung.*, **31** : 167.

Platyseiine mites with the " posterior dorsal shield " bearing fifteen pairs of setae of which five pairs belong to the J series; S series also comprising five pairs. Dorsal setae usually simple, rarely pilose. Lateral margins of the dorsal shield entire or incised. Sternal shield in the female with three pairs of setae; metasternals free. Genital shield wedge shaped and bearing a pair of setae. Ventri-anal shield large with two or more pairs of pre-anals. Peritreme with or without poststigmatic process. Leg I rarely without ambulacrum, usually with at least two claws. Legs II–IV with normal ambulacrum.

This is, at present, the largest genus of the subfamily. A number of the older species are inadequately described and must remain *species incertae sedis* until the type material can be re-examined. The following key includes only those species we have examined.

Type species ***Sejus viduus*** C. L. Koch, 1839

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[1] pp. 73–132 of the third Heft were published in 1843 although most authors consider the complete Heft to have appeared in 1842.

KEY TO THE SPECIES IN THE BRITISH MUSEUM (NATURAL HISTORY)—FEMALES

1. Dorsal shield with lateral incisions (Text-figs. 114 and 168) 2
   —Lateral margins of the dorsal shield entire 3
2. Lateral incisions located anterior to setae S1 and coinciding with their position in the deutonymph (Text-fig. 114); median process of tectum long, Y-shaped (Text-fig. 117); vertical setae absent; ventri-anal shield with one pair of preanals (Text-fig. 116). Sikkim . . . . . *S. clayi* sp. nov. (p. 73)
   —Lateral incisions wide and situated between S2 and S3 (Text.-fig 168); median process of tectum not Y-shaped; vertical setae present; ventrianal shield with two pairs of preanals (Text-fig. 169). Argentina . *S. ornatus* sp. nov. (p. 88)
3. Tarsus I without ambulacrum (Text-fig. 12) 4
   —Tarsus I with ambulacrum or at least with two distinct claws 6
4. Vertical setae considerably longer than i2 (Text-fig. 53); poststigmatic process of the peritreme extending posterior to coxa IV (Text-fig. 54). Europe *S. viduus* C. L. Koch. (p. 52)
   —Vertical setae shorter than i2 (Text-fig. 162); poststigmatic process very short or absent 5
5. With a short but conspicuous poststimatic process of the peritreme; sternal shield with an elongate reticulated area (Text-fig. 164). Sikkim and Argentina *S. browningi* sp. nov. (p. 86)
   —Without a poststigmatic process; sternal shield without such ornamentation (Text-fig. 144). Jamaica . . . . *S. hulli* sp. nov. (p. 81)
6. Peritreme not produced posterior to the stigma (Text-fig. 81) *or* poststigmatic process narrow, short, never extending posterior to coxa IV (Text-fig. 154) . 7
   —Poststigmatic portion of the peritreme strongly developed and extending posterior to coxa IV (Text-fig. 56) 17
7. Dorsal shield strongly arched (Text-fig. 79); sternal region not definitely sclerotized (Text-fig. 81); a number of dorsal setae broad, pilose; ventrianal shield with 7 setae. Britain . . . . *S. dromadis* sp. nov. (p. 62)
   —Dorsal shield at the most with a median longitudinal ridge; sternal shield well-sclerotized; dorsal setae simple or lanceolate 8
8. Leg IV greatly elongated, more than twice the length of the dorsal shield (Text-fig. 99); vertical setae prominent, directed anteriorly; ventri-anal shield with 9 setae. E. Africa . . . . *S. phalangioides* sp. nov. (p. 66)
   —Leg IV never more than 1½ times the length of the dorsal shield 9
9. Vertical setae apparently absent (Text-fig. 124); dorsal and ventral shields characteristically ornamented (Text-figs. 124, 125, 129). Jamaica *S. aciculatus* sp. nov. (p. 76)
   —Vertical setae present, prominent, directed anteriorly (Text-fig. 153) . . 10
10. Peritreme with a distinct poststigmatic process (Text-fig. 154) 11
    —Peritreme without a poststigmatic process (Text-fig. 141) 13
11. Dorsal shield with a distinct " tubercle " in the region of setae J4—this indicates the highest point of the median longitudinal ridge (Text-fig. 153); postigmatic portion of peritreme extending to about the middle of coxa IV. Jamaica *S. neborealis* sp. nov. (p. 84)
    —Dorsal shield without tubercle in the region of setae J4 12
12. Vertical setae shorter than j2 (Text-fig. 103); femur, genu and tibia of leg with sharply pointed spine-like setae situated on tubercles along their anterior and posterior margins; ventri-anal shield with 9 setae (Text-fig. 104). E. Africa *S. spinipes* sp. nov. (p. 69)
    —Vertical setae long, about equal in length to j2 (Text-fig. 63); chaetotaxy of leg I normal; ventri-anal shield with 11 setae. Europe *S. borealis* (Berl.) (p. 56)

13. Tarsus I with a long, strong seta situated dorsally towards the middle of the segment (Text-fig. 140) . . . 14
—Tarsus I without such a prominent seta dorsally . . . 15

14. Dorsal shield with a conspicuous tubercle overhanging setae J5 (Text-fig. 158). Jamaica . . . *S. nodosus* sp. nov. (p. 85)
—Dorsal shield without a tubercle in the region of setae J4 and J5 (Text-fig. 138). Jamaica . . . *S. bellingeri* sp. nov. (p 81).

15. Ventri-anal shield broad, gently rounded posteriorly (Text-fig. 92) ; peritrematal shield not developed posterior to coxa IV. E. Africa . *S. kennedyi* sp. nov. (p. 65)
—Ventri-anal shield markedly tapering in its posterior half (Text-figs. 121 and 132), subtriangular in outline . . . 16

16. Sternal shield with a distinct reticulated area medially ; pre-endopodal shields absent ; paranal setae situated on a strongly-sclerotized bar (Text-fig. 132). Jamaica . . . *S. antillanus* sp. nov. (p. 78)
—Sternal shield without reticulated area ; pre-endopodal shields present (Text-fig. 121) ; paranals not on sclerotized bar. Indonesia . *S. alstoni* sp. nov. (p. 74)

17. Claws on leg I large, sessile (Text-fig. 14) ; tarsus I with a thick spine on its anterior margin. Europe . . . *S. unguiculatus* (Berl.) (p. 53)
—Claw on leg I normal, usually situated on a pretarsus, if sessile claws minute (Text-fig. 13) . . . 18

18. Surface of dorsal shield minutely punctured or tuberculated (Text-fig. 55), reticulation when present restricted to the lateral margins of the shield . . . 19
—Surface of the dorsal shield reticulated, often scabrid, without punctures (Text-fig. 74) . . . 20

19. Dorsal shield minutely punctured (Text-fig. 55) ; sternal shield with an oval reticulated area (Text-fig. 56) ; ventri-anal shield with 11 setae. Europe *S. laelaptoides* (Berl.) (p. 54)
—Dorsal shield tuberculated (Text-fig. 174) ; sternal shield lacking a reticulated area ; ventri-anal shield with 9 setae (Text-fig. 175). Argentina *S. tuberculatus* sp. nov. (p. 89)

20. Claws on leg I minute, apparently sessile ; leg I long and slender, about 1½ times the length of the dorsal shield . . . 21
Claws on leg I situated on a short but distinct pretarsus ; leg I usually considerably less than 1½ times the length of the dorsal shield . . . 22

21. Tibia and tarsus I approximately equal in length ; tarsus I more than 200μ in length. Jamaica . . . *S. jamaicensis* sp. nov. (p. 83)
—Tibia I distinctly longer than tarsus I ; tarsus I not more than 160μ in length. Nepal . . . *S. nepalensis* sp. nov. (p. 71)

22. Vertical setae long, directed anteriorly (Text-fig. 74) ; dorsal shield heavily ornamented ; tarsus I about twice the length of tibia I. British Isles *S. cassiteridum* sp. nov. (p. 61)
—Vertical setae relatively shorter, directed antero-laterally or posteriorly (Text-figs. 67 and 86) ; vertex not well developed . . . 23

23. Tibia I equal in length to or longer than tarsus I. Europe *S. serratus* (Halbert) (p. 58)
Tibia I distinctly shorter than tarsus I (1 : 1.3–1.7) . . . 24

24. Ventri-anal shield with five subcircular areas arranged crescentically posterior to the paranals (Text-fig. 87) ; small weakly-sclerotized species about 360μ in length. E. Africa . . . *S. areolatus* sp. nov. (p. 64)
Ventri-anal shield without such areas ; larger species 400–800μ in length . . . 25

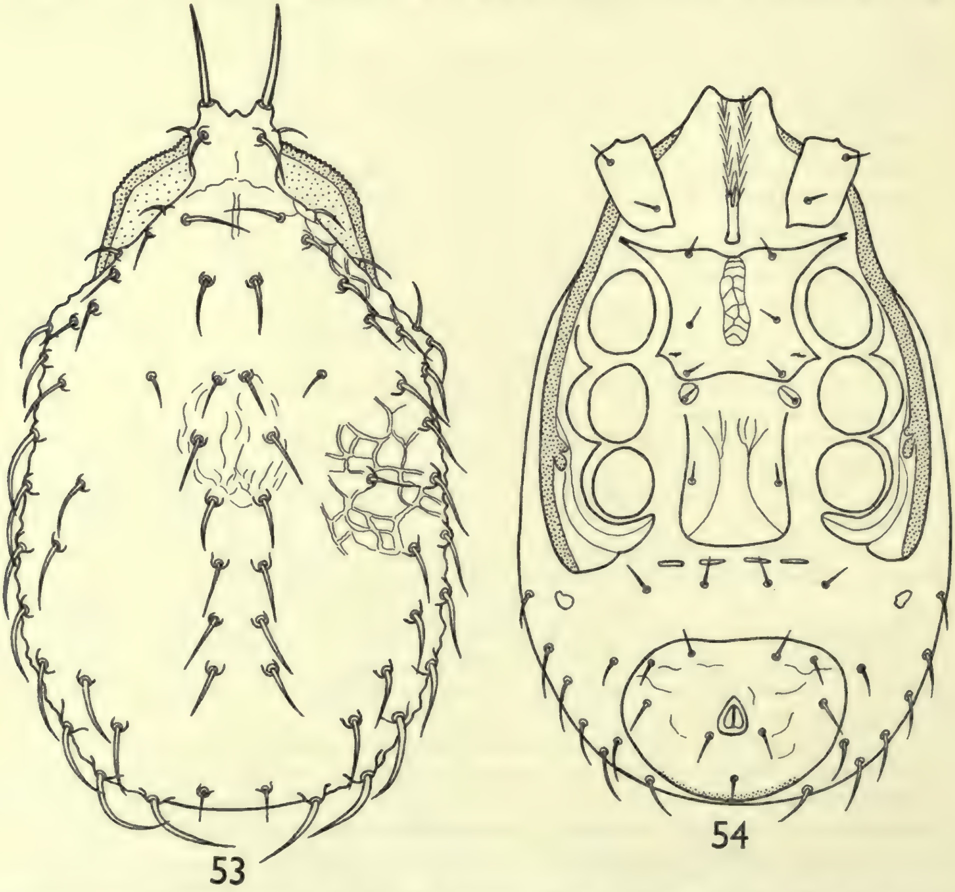
25. J5 about ¾ the length of J4, setiform (Text-fig. 110). Nepal *S. parbatensis* sp. nov. (p. 72)
J5 less than ½ the length of J4, usually thorn-like . . . 26

26. Sternal shield without semicircular depressions near its anterior margin (Text-fig. 71). Europe . . . . *S. curtipes* (Halbert) (p. 59)
—Sternal shield with a pair of semicircular depressions near its anterior margin (Text-fig. 60) 27
27. Sclerotized bases of the vertical setae large, almost contiguous (Text-fig. 59); highest point of median dorsal ridge located between i5. Europe *S. necorniger* (Oudemans) (p. 55)
—Bases of vertical setae weakly sclerotized, widely separated (Text-fig. 100); highest point of median dorsal elevation located between i5 and J1. E. Africa *S. signatus* sp. nov. (p. 68)

Sejus viduus C. L. Koch

Sejus viduus Koch, C. L., 1839, *Deutsch. Crust. Myr. Arach., Fasc.* 24, t. 10.
Epicrius corniger Berlese A., 1891, *A.M.S., Fasc.* 59, No. 2.
Sejus viduus C. L. Koch, Oudemans, A. C., 1936, *K.H.O.A.*, **3A** : 376.
Episeiella heteropoda Willmann, C., 1938, *Ann. Hist. nat. Mus. Hung.*, **31** : 164, syn. nov.

FEMALE. Dorsal shield (529 μ long × 330 μ wide) covered by a strong irregular



FIGS. 53–54. *Sejus viduus* (C. L. Koch), female. Fig. 53, dorsal shield. Fig. 54, venter.

network. Lateral margins irregular. "Anterior dorsal shield" with twenty-one pairs of simple setae; verticals very prominent, well separated, and directed anteriorly. "Posterior dorsal shield" with fifteen pairs of simple setae of which J5 are the shortest. All the setae arise from small protuberances (Text-fig. 53).

Tritosternum with a pair of pilose laciniae. Sternal shield with a reticulated area medially and bearing three pairs of simple setae. Genital shield slightly convex posteriorly and bearing a single pair of simple setae. Ventri-anal shield broader than long (101 μ long × 139 μ wide) with only faint traces of reticulations, and bearing nine simple setae. Between the genital and ventri-anal shields lie four narrow sclerotized platelets. Stigma situated between coxae III and IV; posterior prolongation of peritreme, and peritrematal shield, reaching beyond the posterior margin of coxa IV (Text-fig. 54). Metapodal shields small.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum three-pronged, and chelicerae typical of the genus.

Leg I (724 μ long) with the tarsus (144 μ) shorter than the tibia (167 μ). Setae on tarsus, tibia and genu I very fine; tarsal claws absent; remaining setae stouter. Tarsi II–IV with a pair of lanceolate setae; ambulacra without acuminate lobes.

MALE. Unknown.

DISTRIBUTION. Koch's (1839) description is based on material from wet woodland habitats in Germany. Berlese's (1891) description of *Epicrius corniger* is based on several specimens in moss on high mountains, Venice. Berlese's type has been examined by us in Florence. Willmann's (1939) description of *Episeiella heteropoda*, was made from one female sifted at Vihnyei völgy, Hungary, and is the specimen from which our description and figures are made.

Sejus unguiculatus Berlese

Sejus unguiculatus Berlese, A., 1887, *A.M.S.*, 41, No. 4.
Lasioseius (*Cheiroseius*) *unguiculatus* Berlese, A., 1916, *Redia*, **12** : 33.

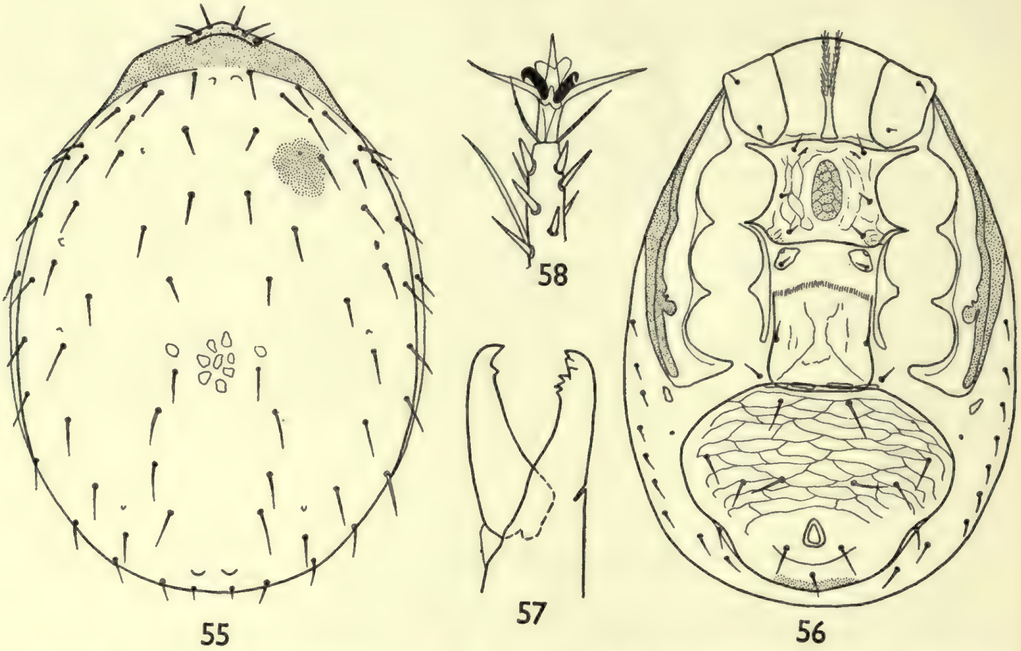
The characteristic feature of this species is that the claws on tarsus I are greatly enlarged and sessile (Text-fig. 14). The chaetotaxy of the dorsal shield is typical of the genus. The "posterior dorsal shield" bears fifteen pairs of setae; five pairs in the J series. The "anterior dorsal shield" bears twenty pairs of setae; vertex weakly developed. The chaetotaxy and sclerotization of the venter are typical of *Sejus*. Sternal shield with three pairs of setae; genital shield with one pair of setae; ventri-anal shield large, occupying most of the area posterior to coxae IV, and bearing eleven simple setae. Six small plates are situated between the genital and ventri-anal shields. Peritreme extending posterior to coxa IV. Metapodal plates conspicuous.

Berlese described this species from moss in Venice. The above description is based on drawings of the type. This species is not represented in the Museum Collections.

Sejus lælaptoides (Berlese) comb. nov.

Epicrius laelaptoides Berlese, A., 1887, *A.M.S.*, *Fasc.* 40, *No.* 10.
Parasejus glaber var. *minor* Trägårdh, I., 1910, *Naturw. Untersuch. Sarekgeb.*, **4** : 432, syn. nov.
Lasioseius (*Episeius*) *sphagni* Halbert, J. N., 1923, *J. Linn. Soc. Lond.* (*Zool.*), **35** : 371, syn. nov.

FEMALE. Dorsal shield (518–581 μ long × 330–415 μ wide) minutely punctured and with a few faint scattered reticulated areas (Text-fig. 55). "Anterior dorsal shield" with twenty-one pairs of simple setae ; verticals well separated and directed anteriorly. "Posterior dorsal shield" with fifteen pairs of simple setae ; J5 very short. The distribution and relative lengths of the dorsal setae, and the ornamentation of the dorsal shield are shown in the Text-fig.



FIGS. 55–58. *Sejus laelaptoides* (Berlese), female. Fig. 55, dorsum. Fig. 56, venter. Fig. 57, chelicera. Fig. 58, tarsus II.

Tritosternum well developed with pilose laciniae. Sternal shield with a conspicuous elliptical reticulated area, and bearing three pairs of simple setae (Text-fig. 56). Genital shield broad, posterior margin straight, and bearing one pair of simple setae. Ventri-anal shield large, broader than long (152–215 μ long × 240–291 μ wide), reticulated, and bearing eleven simple setae. Between the genital and ventri-anal shields lies a row of four narrow sclerotized plates. Stigma situated between coxae III and IV ; peritreme and peritrematal shield extending posterior to coxa IV. Metapodal plates small.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum three-pronged and typical of the genus. The dentition of the chelicera is shown in Text-fig. 57.

Leg I (536–673 μ long) with the tarsus (113–126 μ) longer than the tibia (104–118 μ). Setae on tarsus and tibia fine, those on other segments somewhat stouter; tarsal claws strong. Tarsi II–IV with a pair of lanceolate setae; ambulacra with three acuminate lobes (Text-fig. 58).

MALE. Unknown.

DISTRIBUTION. Berlese (1887) described *Epicrius laelaptoides* from the Royal Botanic Gardens, Padua. Trägårdh (1910) described *Parasejus glaber* var. *minor* from *Sphagnum* at Sarekgebirge, Sweden, and Halbert (1923) described *Lasioseius* (*Episeius*) *sphagni* from *Sphagnum* in Co. Dublin, Eire. The writers have examined Berlese's type in Florence, Halbert's type, and also numbers of females from Whernside Moor, Cock Hill, and Malham Tarn, Yorkshire; Rydal Water and Grasmere, Westmorland; Leith Hill and Beckley, Surrey; Lapland; and Michigan.

Sejus necorniger (Oudemans) comb. nov.

Hypoaspis necorniger Oudemans, A. C., 1903, *Ent. Ber.*, **1**, 12 : 87.
Platyseius necorniger, Buitendijk, A. M., 1945, *Zool. Med.*, **24** : 296.
Episeius necorniger, Willmann, C., 1949, *Veröff. Mus. Nat. Bremen, No. 1A* : 120.
Episeius necorniger, Willmann, C., 1952, *Veröff. Inst. Meeresf. Bremerhaven*, **1** : 148.

FEMALE. Dorsal shield (550–722 μ long × 320–467 μ wide) completely covered by a fine reticulated pattern (Text-fig. 59). "Anterior dorsal shield" with twenty-one pairs of simple setae; verticals, with their bases close together, considerably shorter than post-verticals. "Posterior dorsal shield" with fifteen pairs of simple setae. The distribution of the setae and the ornamentation of the dorsal shield are shown in the Text-fig.

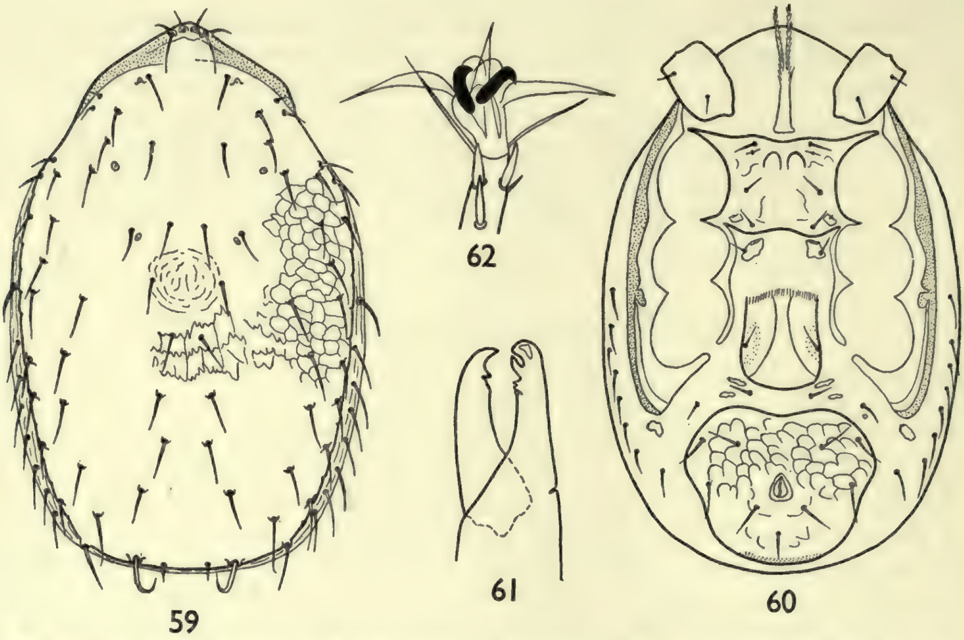
Tritosternum well developed with pilose laciniae. Sternal shield with some sculpturing, and with two semicircular marks anteriorly, and bearing three pairs of simple setae (Text-fig. 60). Genital shield convex posteriorly and bearing a single pair of setae. Ventri-anal shield slightly wider than long (162–190 μ long × 177–228 μ wide), reticulated, and bearing nine simple setae. Between the genital and ventri-anal shields lie four small sclerotized plates. Stigma situated between coxae III and IV; peritreme extending posterior to coxa IV. Metapodal plates narrow.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum three-pronged and typical of the genus. The dentition of the chelicera is shown in Text-fig. 61.

Leg I (578–782 μ long) with the tarsus (144–184 μ) longer than the tibia (101–126 μ); claws small, pulvillus short. Setae on tarsus and tibia fine, those on remaining segments stouter. Tarsi II–IV with a pair of lanceolate setae; ambulacra with three acuminate lobes (Text-fig. 62).

MALE. Unknown.

Distribution. Oudemans (1903) did not state the locality for his type female, but Buitendijk (1945) in his catalogue of the Oudemans Collection gives the locality as Borkum Island, Germany. Willmann (1952) records the species from the North Sea island of Wangerooge, and says it is found as far up as Lapland. We have examined specimens from the following localities : Kirkstone Pass, River Brathey and High Pike, Ambleside, Westmorland ; Rambulls Moor, Ilkley, Yorkshire ; Hathersage, Derbyshire ; Sea Houses, Northumberland ; Burton Marsh, Cheshire ; Llyn Idwal, Caernarvonshire ; South Wales ; Washford, Somerset ; Kiel, Germany ; Ohrid, Montenegro ; and Grabouw, Transvaal.



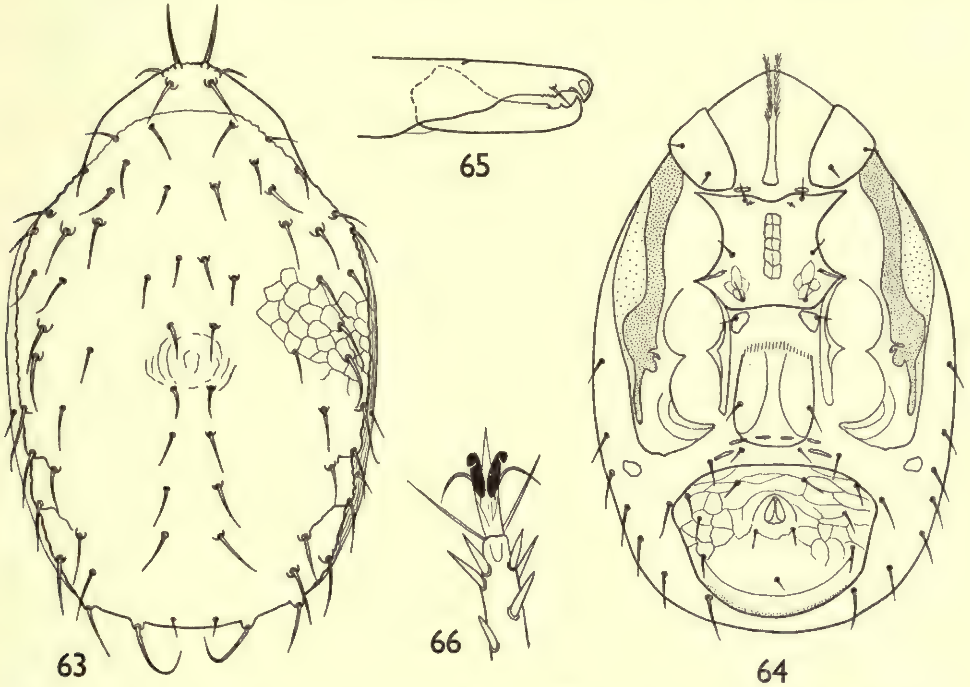
Figs. 59–62. *Sejus necorniger* (Oudemans), female. Fig. 59, dorsum. Fig. 60, venter. Fig. 61, chelicera. Fig. 62, tarsus II.

Sejus borealis (Berlese) comb. nov.

Ameroseius borealis Berlese, A., 1904, *Redia*, **1** : 259.
Episeius montanus Willmann, C., 1949, *Veröff. Mus. Nat. Bremen, No. 1A* : 120. syn. nov.
Episeius montanus Willmann, C., 1952, *Veröff. Inst. Meeresf. Bremerhaven*, **1** : 148.
Episeius montanus Willmann, C., 1952, *SB. öst. Akad. Wiss., Abt.* 1, **162** : 462.

Female. Dorsal shield (570–581 μ long × 361–371 μ wide) covered by a reticulated pattern (Text-fig. 63). "Anterior dorsal shield" bears twenty-one pairs of simple setae ; verticals anteriorly projected. "Posterior dorsal shield" bears fifteen pairs of simple setae ; J5 are at the most half the length of J4. The majority of the dorsal setae arise from small tubercles. The distribution and relative length of the setae and the ornamentation of the dorsal shield are shown in the Text-fig.

Tritosternum well developed and flanked at its base by a pair of narrow pre-endopodal shields. Sternal shield with a narrow longitudinal reticulated area, and bearing three pairs of simple setae (Text-fig. 64). Genital shield convex posteriorly and bearing a single pair of setae. Ventri-anal shield broader than long (139–164 μ long × 202–205 μ wide), reticulated and bearing eleven simple setae. Between the genital and ventri-anal shield lies a row of four small plates, and, posterior to these, two smaller plates. Stigma situated between coxae III and IV with the posterior prolongation of the peritreme extending to about the middle of coxa IV. Metapodal plates circular.



Figs. 63–66. *Sejus borealis* (Berlese), female. Fig. 63, dorsum. Fig. 64, venter. Fig. 65, chelicera. Fig. 66, tarsus II.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum three-pronged and typical of the genus. The dentition of the chelicera is shown in Text-fig. 65.

Leg I (576–580 μ long) with the tarsus (137–139 μ) longer than the tibia (108–114 μ). Setae on tarsus and tibia I fine ; ambulacrum and claws small ; remaining setae stouter and arising from small protuberances. Tarsi II–IV with a pair of lanceolate setae, and ambulacra with three acuminate lobes (Text-fig. 66). Setae of legs II–IV arising mainly from small protuberances.

MALE. Unknown.

DISTRIBUTION. Berlese's (1904) description of the female of *Ameroseius borealis* is based on material collected by Thor in Norway. His type specimen has been examined by us. Willmann (1949) described *Episeius montanus* from Poland; in 1952 he recorded the species from the North Sea island of Wangerooge, and in 1953 he recorded it from several localities in the eastern Alps. The writers have examined five females from Soil Insecticide Experiment, Bellahouston Park, Glasgow, October, 1951, collected by J. G. Sheals; one female from ditch-side debris near Markfield, Leicestershire, 19.iv.1958, collected by P. N. Lawrence; and one female from wet moss at West Carter Basin, Labrador, 17.viii.1958, also collected by P. N. Lawrence.

Sejus serratus (Halbert) comb. nov.

Paraseius serratus Halbert, J. N., 1915, *Proc. R. Irish Acad.*, **39**ii : 78.
Lasioseius (*L.*) *serratus*, Schweizer, J., 1922, *Ver. naturf. Ges. Basel*, **33** : 43.
Episeius serratus, Schweizer, J., 1949, *Rés. Rech. sci. Parc Nat. Suisse, N.F.* **2** : 63.
Episeius serratus, Willmann, C., 1949, *Veröff. Mus. Bremen*, **1**A : 120; 1954, In *Spiegel, Land-Tierwelt*, 15 *Ordnung, Acarina* : 351.

FEMALE. Dorsal shield (440–570 μ long × 286–351 μ wide) with a pattern of irregular reticulations and depressions (Text-fig. 67). "Anterior dorsal shield" with twenty-one pairs of simple setae; verticals on small tubercles and directed laterally. "Posterior dorsal shield" with fifteen pairs of simple setae. The distribution of the dorsal setae and the ornamentation of the dorsal shield are shown in the Text-fig.

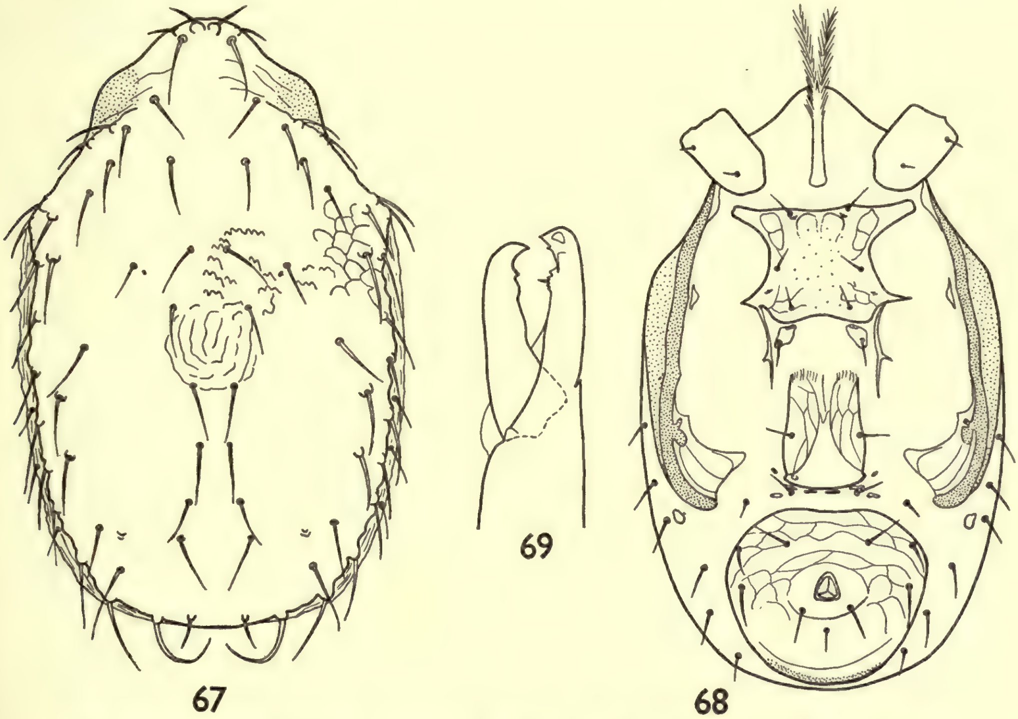
Tritosternum with a narrow base and pilose laciniae. Sternal shield with some sculpturing laterally, with a pair of circular marks anteriorly, and bearing three pairs of simple setae (Text-fig. 68). Genital shield convex posteriorly and bearing a single pair of setae. Ventri-anal shield slightly wider than long (152–170 μ long × 165–200 μ wide), reticulated anteriorly and bearing nine simple setae. Between the genital and ventri-anal shields lie a row of small plates and behind these a further pair. Stigma situated between coxae III and IV; peritreme extending posterior to coxa IV. Metapodal plates small.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum three-pronged and typical of the genus. The dentition of the chelicera is shown in Text-fig. 69.

Leg I (528–718 μ long) with the tarsus (121–149 μ) shorter than the tibia (139–164 μ). Claws on leg I small; pulvillus short. Setae on tarsus and tibia fine; those on remaining segments stouter. Tarsi II–IV with a pair of lanceolate setae; ambulacra with three acuminate lobes.

MALE. This sex is described and figured by Schweizer (1922 & 1949).

DISTRIBUTION. Halbert (1915), in the Clare Island Survey, described this species from specimens "Found commonly in sphagnum, gathered on the slopes of Croaghpatrick at an elevation of about 600 ft., during the month of October". Schweizer (1922 & 1949) records both sexes from the Swiss Alps, and Willmann (1954) records the female from Austria. The Museum Collections contain the following specimens: one female in *Sphagnum* from marsh, Raise Beck, Grasmere, Westmorland, 900 ft., 29.vi.1951, collected by J. T. Salmon; three females in mosses and liverworts on rocks by south-east bank of Rydal Water, Westmorland, 29.vi.1956, collected by P. N. Lawrence; one female in *Sphagnum* at Blelham Tarn, Lancashire, 22.iii.1955, collected by R. J. Elliott; one female in *Sphagnum* at Box Hill, Surrey, 30.vi.1951, collected by E. Duffey; and two females in moss at West Carter Basin, Labrador, 7.viii.1958, collected by P. N. Lawrence.



FIGS. 67–69. *Sejus serratus* (Halbert), female. Fig. 67, dorsum. Fig. 68, venter. Fig. 69, chelicera.

Sejus curtipes (Halbert) comb. nov.

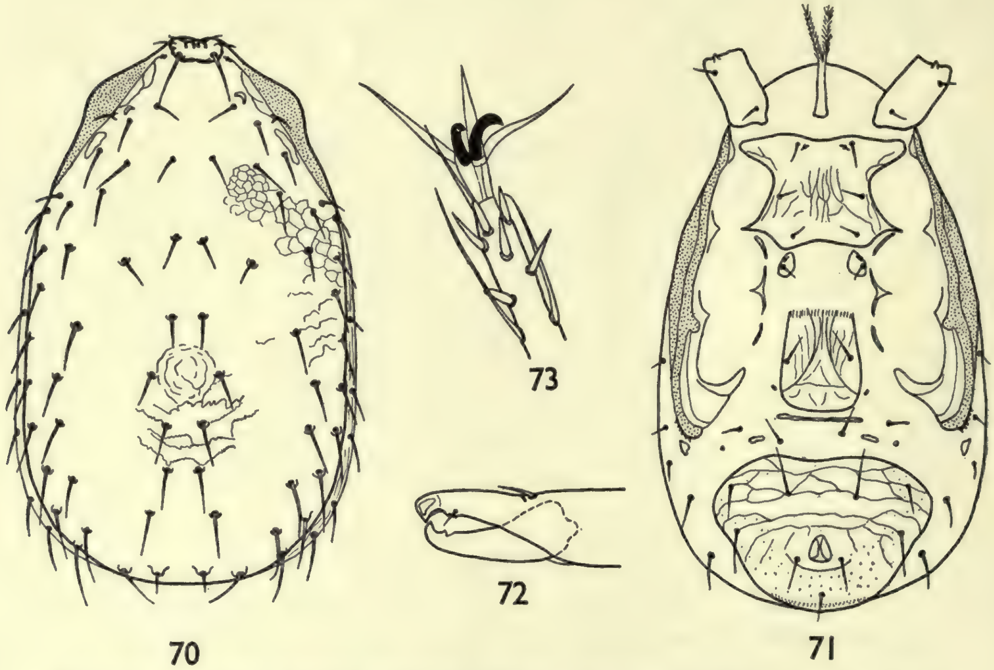
Lasioseius (*Episeius*) *glaber* var. *curtipes* Halbert, J. N., 1923., *J. Linn. Soc. Lond.* (*Zool.*), **35**: 370.

Episeius ovaspini Schweizer, J., 1949, *Rés. Rech. sci. Parc Nat. Suisse, N.F.* **2**: 69, syn. nov.

FEMALE. Dorsal shield (456–529 μ long × 258–320 μ wide) with a reticulated pattern (Text-fig. 70). " Anterior dorsal shield " with fifteen pairs of simple setae.

The distribution of the setae, and the ornamentation of the dorsal shield are shown in the Text-fig.

Tritosternum with pilose laciniae. Sternal shield very faintly sculptured and bearing three pairs of simple setae (Text-fig. 71). Genital shield convex posteriorly and bearing a single pair of setae. Ventri-anal shield wider than long (120–160 μ long × 154–218 μ wide), reticulated in its anterior half, and bearing nine simple setae. Between the genital and ventri-anal shields lies a pair of long narrow platelets and behind these two shorter platelets. Stigma situated between coxae III and IV; peritreme extending posterior to coxa IV. Metapodal plates small.



FIGS. 70–73. *Sejus curtipes* (Halbert), female. Fig. 70, dorsum. Fig. 71, venter. Fig. 72, chelicera. Fig. 73, tarsus II.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum three-pronged and typical of the genus. The dentition of the chelicera is shown in Text-fig. 72.

Leg I (443–518 μ long) with the tarsus (113–139 μ) longer than the tibia (68–88 μ). Claws on leg I small, pulvillus short; setae on tarsus and tibia fine, those on remaining segments stouter. Tarsi II–IV with a pair of lanceolate setae; ambulacra with three acuminate lobes (Text-fig. 73).

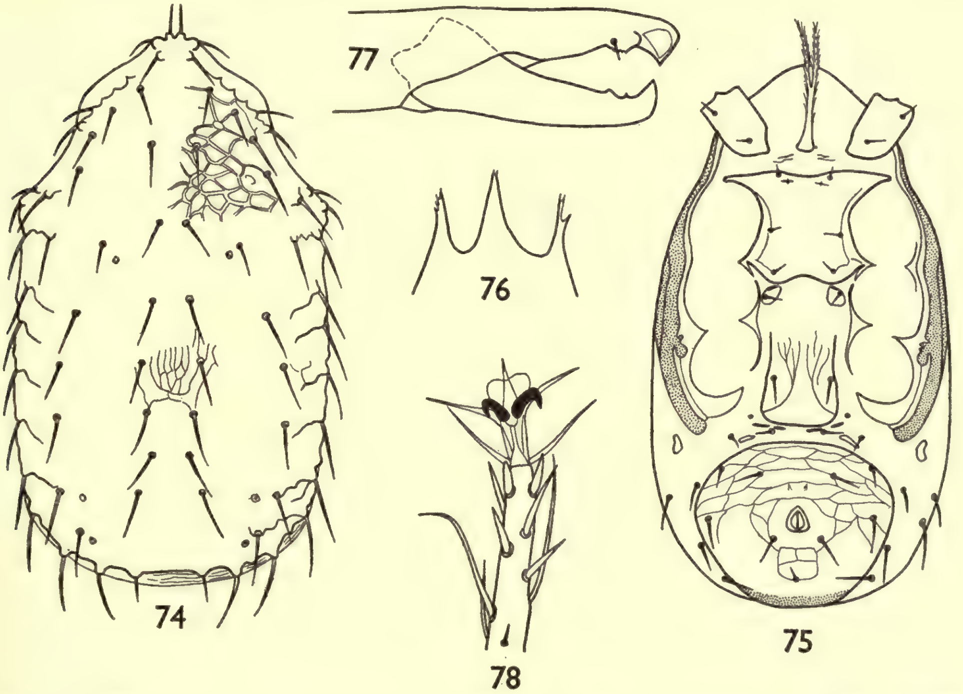
MALE. This sex is described and figured by Schweizer (1949 : 71).

DISTRIBUTION. Halbert's (1923) description of *Lasioseius* (*Episeius*) *glaber* var.

curtipes is based on two females found amongst wet moss on Lambay Island, Co. Dublin, in July. Schweizer's (1949) description of *Episeius ovaspini* is based on five males and thirty-two females collected in wet mosses in the Swiss National Park. We have examined Halbert's type and a number of Schweizer's type series; also five females from the summit of Snowdon, Caernarvonshire, August, 1951, collected by E. Duffey; and eleven females from Jamaica, B.W.I., collected by P. F. Bellinger; seven in moss on concrete, Coolsbade, Portland, 17.vii.1955, and four in moss, west side of John Cove Mountains, 2,300 ft., 25.v.1956.

Sejus cassiteridum sp. nov.

FEMALE. Dorsal shield (435–467 μ long × 237–258 μ wide) heavily sculptured and with a network of ridges and depressions. Lateral margins irregular (Text-fig. 74). "Anterior dorsal shield" with twenty-one pairs of simple setae; verticals close together and projecting anteriorly. "Posterior dorsal shield" with fifteen pairs of simple setae of which J5 are the shortest. The distribution and relative lengths of the dorsal setae and the ornamentation of the dorsal shield are shown in the Text-fig.



FIGS. 74–78. *Sejus cassiteridum* sp. nov., female. Fig. 74, dorsum. Fig. 75, venter. Fig. 76, tectum. Fig. 77, chelicera. Fig. 78, tarsus II.

Tritosternum well developed with pilose laciniae. Sternal shield almost entirely without sculpturing, and bearing three pairs of short simple setae (Text-fig. 75). Genital shield slightly convex posteriorly and bearing a single pair of setae. Ventri-anal shield wider than long (115–139 μ long × 152–165 μ wide), reticulated and bearing nine simple setae. Between the genital and ventri-anal shields lie six small sclerotized plates. Stigma situated between coxae III and IV; peritreme and peritrematal shields extending posterior to coxa IV. Metapodal plates small.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum (Text-fig. 76) three-pronged. The dentition of the chelicera is shown in Text-fig. 77.

Leg I (372–387 μ long) with the tarsus (99–106 μ) almost twice the length of the tibia (58–63 μ). Setae on tarsus and tibia fine, those on other segments stouter; pulvillus short and tarsal claws small. Tarsi II–IV with a pair of lanceolate setae; ambulacra with three acuminate lobes (Text-fig. 78).

MALE. Unknown.

LOCALITY. England. The holotype female (1959.1.20.92) and twenty-five paratype females (1959.1.20.93–102) occurring with *Platyseius subglaber* (Oudemans) in the roots of rushes by Big Pool, St. Agnes, Isles of Scilly, Cornwall, 19.ix.1957, collected by K. H. Hyatt.

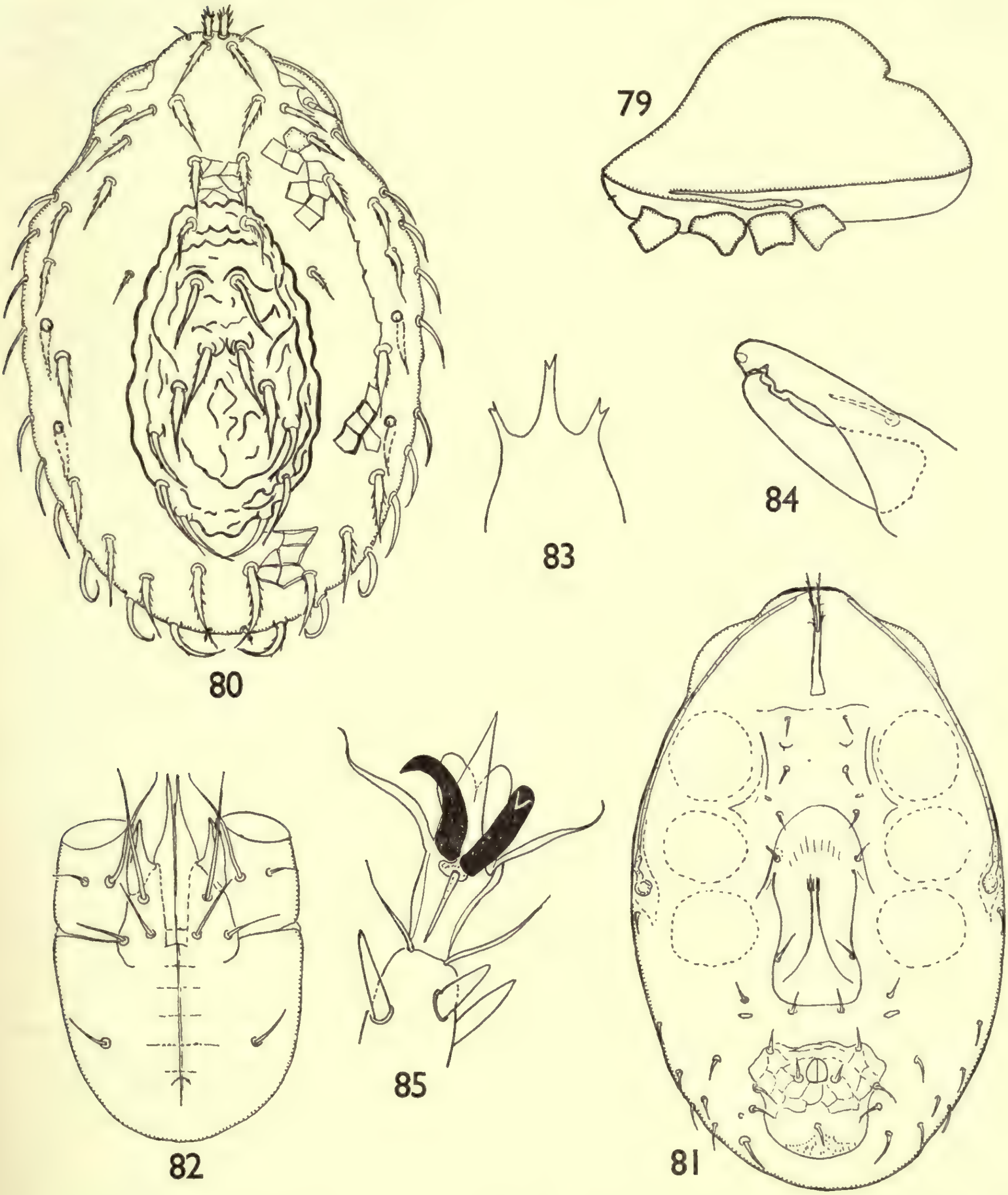
The writers have examined a single female (1959.1.20.193) from *Sphagnum*, Blelham Tarn, Windermere, Lancashire, 22.iii.1955, collected by R. J. Elliott, which differs from the St. Agnes specimens by having the sternal shield conspicuously reticulated. The measurements of this specimen all fall within the ranges given above for *Sejus cassiteridum* (viz.: dorsal shield 446 × 247 μ, ventri-anal shield 126 × 157 μ, leg I 392 μ, tarsus I 101 μ, tibia I 63 μ).

Sejus dromadis sp. nov.

FEMALE. Dorsal shield (393 μ long × 230 μ wide) oval in outline, heavily reticulated, and steeply humped dorso-medially (Text-fig. 79). "Anterior dorsal shield" with twenty-three pairs of setae; "posterior dorsal shield" with fifteen pairs of setae (Text-fig. 80). The verticals are stout and spiculate, and the remainder of the setae are stout and pilose. The distribution and relative lengths of the dorsal setae, and the form of the dorsal shield are shown in the Text-figs.

Tritosternum less strongly developed than in the majority of species of *Sejus*. Laciniae pilose. Sternal shield weakly sclerotized with three pairs of simple setae. Genital shield broadly flask-shaped with one pair of setae (Text-fig. 81). Ventri-anal shield small (83 μ long × 88 μ wide), weakly sclerotized, and bearing seven simple setae. Two small sclerotized plates lie on the interscutal membrane between the genital and ventri-anal shields. Stigma situated between coxae III and IV, with the peritreme not extending posterior to the stigma. Peritrematal shield extending a little posterior to the stigma.

Venter of gnathosoma with rostral and internal palptrochanter setae long and whip-like (Text-fig. 82). All setae on pedipalp simple. Tectum three-pronged and



FIGS. 79–85. *Sejus dromadis* sp. nov., female. Fig. 79, lateral view of dorsum. Fig. 80, dorsal shield. Fig. 81, venter. Fig. 82, venter of gnathosoma. Fig. 83, tectum. Fig. 84, chelicera. Fig. 85, tarsus II.

typical of the genus (Text-fig. 83). The dentition of the chelicera is shown in Text-fig. 84.

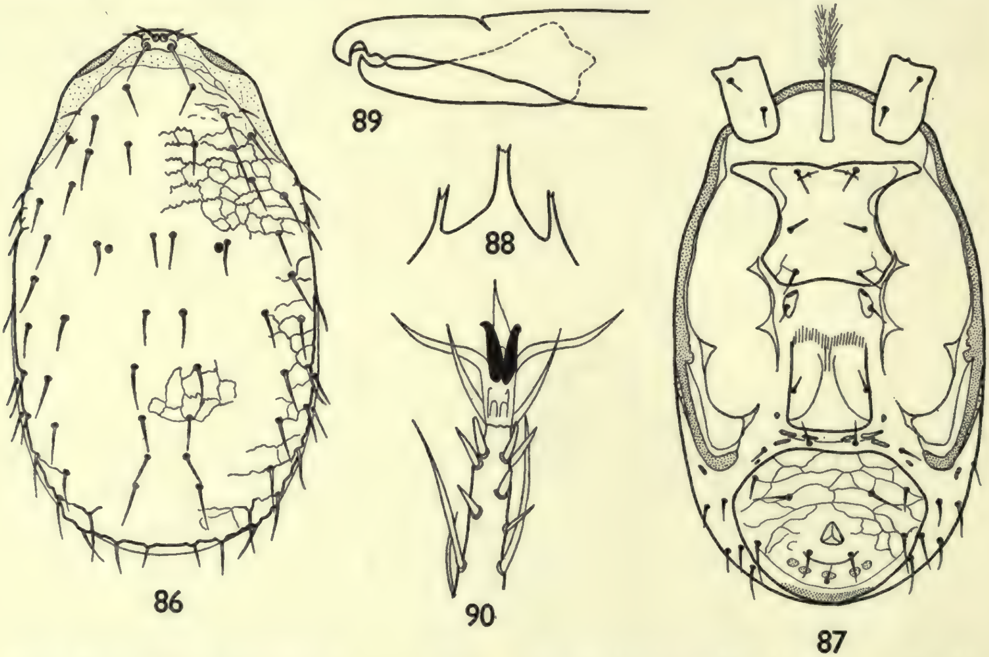
Leg I (about 300 μ long) with the tarsus (70 μ) longer than the tibia (56 μ). Setae on tarsus fine; those on remaining segments stouter, and in some cases spiculate and arising from small protuberances. Tarsi II–IV with a pair of lanceolate setae. Ambulacrum of tarsus I short and claws small. Pulvilli of tarsi II–IV produced into three acuminate lobes (Text-fig. 85).

MALE. Unknown.

LOCALITY. England. A single female (1959.1.20.103) in cow dung at Canterbury, Kent, collected by the late Dr. E. Warren.

Sejus areolatus sp. nov.

FEMALE. Dorsal shield (361 μ long × 216 μ wide) completely covered by a fine reticulated pattern; margin irregular (Text-fig. 86). "Anterior dorsal shield" with twenty-one pairs of simple setae; verticals with their bases touching, and considerably shorter than post-verticals. "Posterior dorsal shield" with fifteen pairs of simple setae. The distribution of the setae and the ornamentation of the dorsal shield are shown in the Text-fig.



FIGS. 86–90. *Sejus areolatus* sp. nov., female. Fig. 86, dorsum. Fig. 87, venter. Fig. 88, tectum. Fig. 89, chelicera. Fig. 90, tarsus II.

Tritosternum well developed with pilose laciniae. Sternal shield almost plain, with three pairs of simple setae (Text-fig. 87). Genital shield bearing a single pair of setae. Ventri-anal shield wider than long (106 μ long × 132 μ wide), reticulated, with five small oval areas forming a crescent behind the paranals, and bearing nine simple setae. Between the genital and ventri-anal shields lies a row of four sclerotized platelets, and behind these two smaller ones. Stigma situated between coxae III and IV ; peritreme extending posterior to coxa IV. Metapodal plates small and narrow.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum three-pronged (Text-fig. 88), the centre prong being in advance of the lateral ones. The dentition of the chelicera is shown in Text-fig. 89.

Leg I (c. 330 μ long) with the tarsus (88 μ) longer than the tibia (50 μ). Setae on tarsus and tibia fine, those on remaining segments stouter ; claws small, on short pulvillus. Tarsi II–IV with a pair of lanceolate setae ; ambulacra with three acuminate lobes (Text-fig. 90).

MALE. Unknown.

LOCALITY. Uganda. A single female, the holotype (1959.1.20.104), from rushes and grassland bordering hot springs, sixteen miles east-north-east of Bundibugyo, Ruwenzori, 29.viii.1952, collected by G. Owen Evans.

Sejus kennedyi sp. nov.

FEMALE. Dorsal shield (456–467 μ long × 268–279 μ wide) covered by a network of small depressions and ridges (Text-fig. 91). " Anterior dorsal shield " with twenty-one pairs of simple setae ; verticals separated by the width of their bases and projecting anteriorly. " Posterior dorsal shield " with fifteen pairs of simple setae of which J5 are short. The distribution and relative lengths of the dorsal setae and the ornamentation of the dorsal shield are shown in the Text-fig.

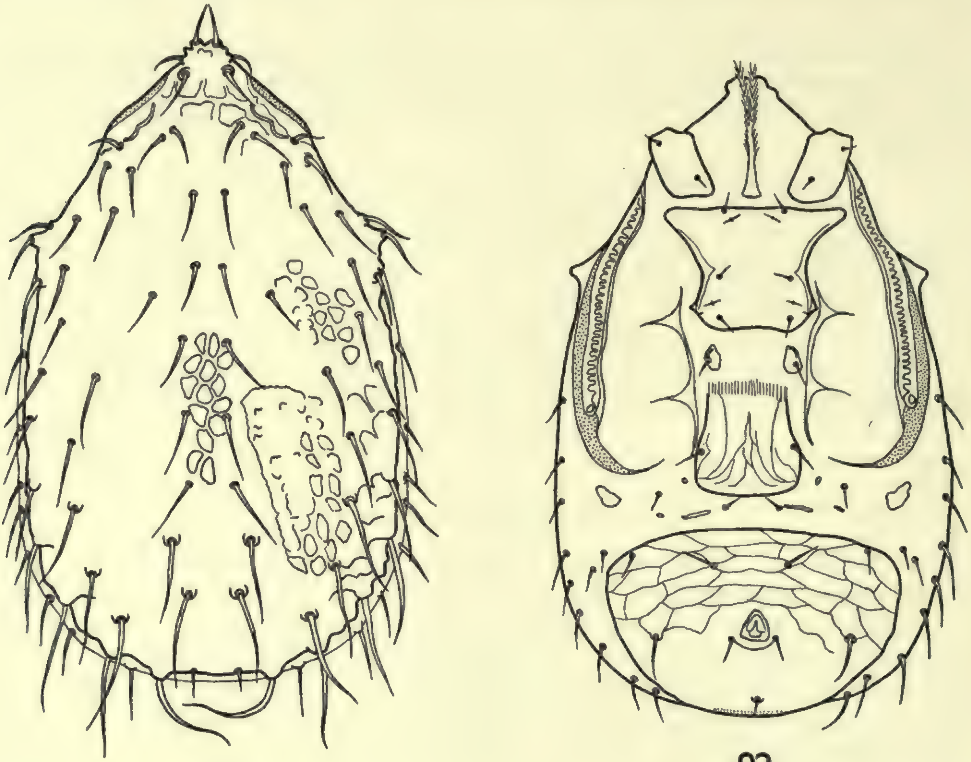
Tritosternum with a pair of pilose laciniae. Sternal shield plain and bearing three pairs of simple setae (Text-fig. 92). Genital shield lightly reticulated, convex posteriorly, and bearing one pair of simple setae. Ventri-anal shield broader than long (139–144 μ long × 208–213 μ wide), reticulated, and bearing nine simple setae. Between the genital and ventri-anal shields lie two narrow sclerotized platelets. Stigma situated between coxae III and IV ; peritreme crenate along its internal margin, and with no post-stigmal prolongation. Peritrematal shield tapering and extending posterior to coxa IV. Metapodal shields obliquely situated.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum three-pronged and typical of the genus. Chelicerae typical.

Leg I (354 μ long) with the tarsus (88 μ) longer than the tibia (63 μ). Setae on tarsus I fine, ambulacrum and claws small ; setae on remaining segments stouter and arising from small protuberances. Tarsi II–IV with a pair of lanceolate setae and ambulacra with three acuminate lobes.

MALE. Unknown.

LOCALITY. Uganda. The holotype female (1959.1.20.105) and three paratype females (1959.1.20.106–108) from litter under hardwood stand, Bundibugyo, Ruwenzori, 3,400 ft., 2.ix.1952, collected by G. Owen Evans. This species is named after Professor W. Q. Kennedy, University of Leeds, leader of the British Ruwenzori Expedition, 1952.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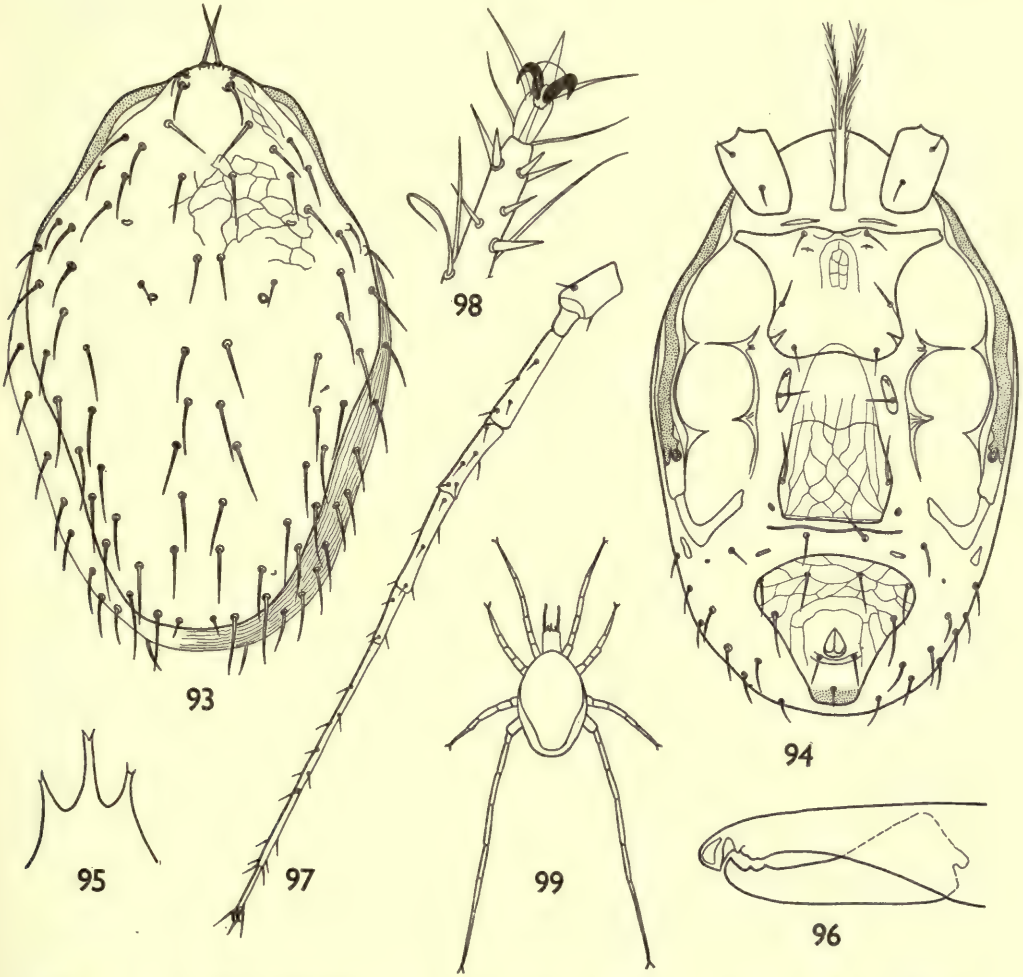
FIGS. 91–92. *Sejus kennedyi* sp. nov., female. Fig. 91, dorsum. Fig. 92, venter.

Sejus phalangioides sp. nov.

FEMALE. Dorsal shield (398–410 μ long × 250–253 μ wide) attenuated in the posterior half, and covered by a fine reticulated pattern (Text-fig. 93). " Anterior dorsal shield " with twenty-one pairs of simple setae, verticals projecting anteriorly ; " posterior dorsal shield " with fifteen pairs of simple setae, of which J5 are the shortest. The distribution and relative lengths of the dorsal setae are shown in the Text-fig.

Tritosternum well developed and flanked at its base by a pair of narrow pre-endopodal shields. Sternal shield with a reticulated area anteriorly, and bearing three pairs of simple setae (Text-fig. 94). Genital shield broad, truncated posteriorly, distinctly reticulated, and bearing a single pair of setae. Ventri-anal shield slightly broader than long (101 μ long × 116 μ wide), attenuated posteriorly, reticulated, and bearing nine simple setae. Between the genital and ventri-anal shields lies a narrow, undulated, sclerotized strip of chitin, and two platelets. Stigma situated between coxae III and IV, peritreme scarcely extending posterior to the stigma.



FIGS. 93–99. *Sejus phalangioides* sp. nov., female. Fig. 93, dorsum. Fig. 94, venter. Fig. 95, tectum. Fig. 96, chelicera. Fig. 97, leg IV. Fig. 98, tarsus II. Fig. 99, entire mite, showing relative lengths of legs and idiosoma.

Peritrematal shield fused with well developed podal plates, which extend posterior to coxa IV. Metapodal plates small, situated close to podal plates.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum (Text-fig. 95) three-pronged and typical of the genus. The dentition of the chelicera is shown in Text-fig. 96.

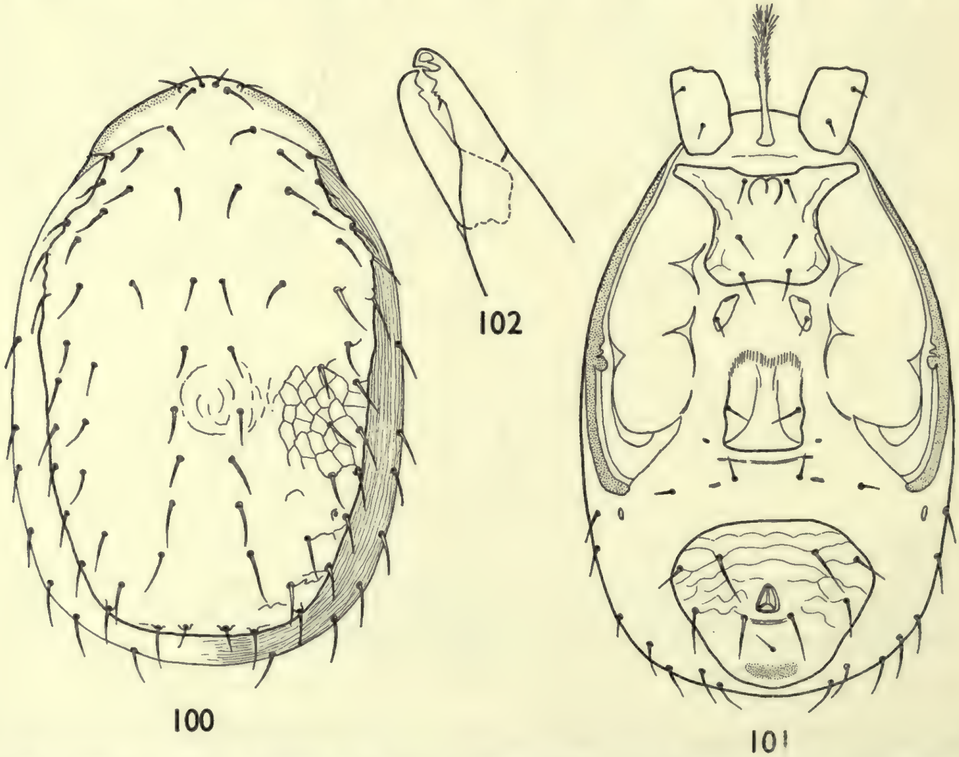
Leg I (536 μ long) has the tarsus (139 μ) longer than the tibia (100–106 μ). Setae on tarsus I very fine; those on remaining segments stouter. Ambulacrum of tarsus I short, claws small. Leg IV (954 μ long) more than twice the length of the idiosoma, with the tarsus about 400 μ long (Text-fig. 97). Tarsi II–III with a pair of lanceolate setae, and pulvilli produced into three acuminate lobes (Text-fig. 98). Tarsus IV without lanceolate setae, and pretarsus long (55 μ). The relative lengths of the legs and the idiosoma are shown in Text-fig. 99.

MALE. Unknown.

LOCALITY. Uganda. The holotype female (1959.1.20.109) and one paratype female (1959.1.20.110) in grassland in forest clearing near stream, nine miles north-east of Bundibugyo, Ruwenzori, 2,850 ft., 24.viii.1952, collected by G. Owen Evans.

Sejus signatus sp. nov.

FEMALE. Dorsal shield (581 μ long × 371 μ wide) weakly sclerotized and covered by a reticulated pattern (Text-fig. 100). "Anterior dorsal shield" with twenty



FIGS. 100–102. *Sejus signatus* sp. nov., female. Fig. 100, dorsum. Fig. 101, venter. Fig. 102, chelicera.

pairs of simple setae ; verticals considerably shorter than post-verticals, and well separated. " Posterior dorsal shield " with fifteen pairs of simple setae. The distribution of the dorsal setae and the ornamentation of the dorsal shield are shown in the Text-fig.

Tritosternum with pilose laciniae. Sternal shield weakly sclerotized, with an M-shaped mark anteriorly and bearing three pairs of simple setae (Text-fig. 101). Genital shield weakly sclerotized and bearing one pair of setae. Ventri-anal shield wider than long (152 μ long × 197 μ wide), weakly sclerotized and bearing nine simple setae. Between the genital and ventri-anal shields lie a narrow sclerotized strip and two platelets. Stigma situated between coxae III and IV ; peritreme extending posterior to coxa IV. Metapodal plates very small.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum three-pronged and typical of the genus. The dentition of the chelicera is shown in Text-fig. 102.

Leg I (573 μ long) with the tarsus (141 μ) longer than the tibia (99 μ). Claws on leg I small, inconspicuous, pulvillus short. Setae on tarsus and tibia fine, those on other segments stouter. Tarsi II–IV with a pair of lanceolate setae ; ambulacra with three acuminate lobes.

MALE. Unknown.

LOCALITY. Uganda. A single female, the holotype (1959.1.20.111), from damp decaying vegetation and soil under elephant-grass at Ibanda, Ruwenzori, 26.vii.1952, 4,760 ft., collected by G. O. Evans.

Sejus spinipes sp. nov.

FEMALE. Dorsal shield (392 μ long × 216 μ wide) covered by a light reticulated pattern (Text-fig. 103). " Anterior dorsal shield " bears twenty-one pairs of simple setae ; verticals anteriorly projecting. " Posterior dorsal shield " bears 15 pairs of simple setae ; J5 are as long as J4. The majority of the dorsal setae arise from small tubercles. The distribution and relative lengths of the dorsal setae, and the ornamentation of the dorsal shield are shown in the Text-fig.

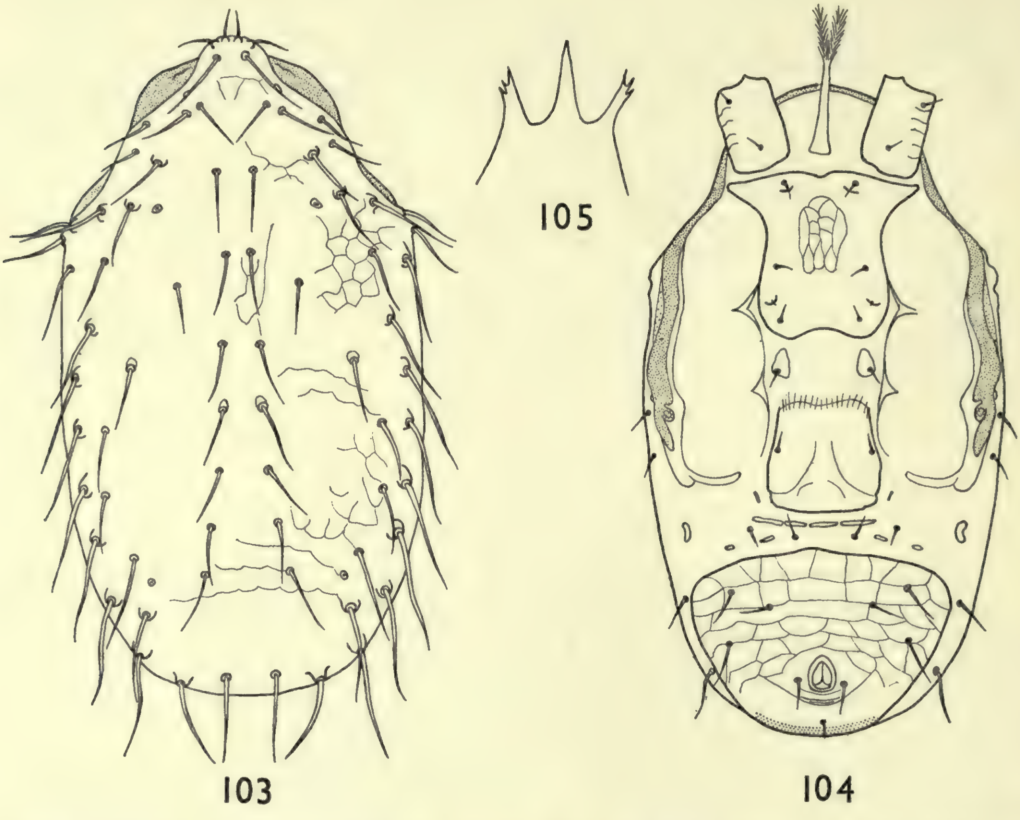
Tritosternum well developed with pilose laciniae. Sternal shield with the central area reticulated, and bearing three pairs of short simple setae (Text-fig. 104). Genital shield with a single pair of simple setae. Ventri-anal shield broader than long (119 μ long × 157 μ wide), distinctly reticulated and bearing nine simple setae. Between the genital and ventri-anal shields lies a line of four contiguous sclerotized plates, and, postero-laterally to these, four smaller plates. Stigma situated between coxae III and IV, with the posterior prolongation of the peritreme extending to about the middle of coxa IV. The peritrematal shield extends posterior to coxa IV. Metapodal plates small.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum (Text-fig. 105) three-pronged. The dentition of the chelicera is typical of the genus.

Leg I (c. 330 μ long) with the tarsus (76 μ) longer than the tibia (53 μ). Setae on tarsus I fine; ambulacrum and claws small; many of the setae on remaining segments stout and arising from conspicuous protuberances. Tarsi II–IV with a pair of lanceolate setae, and ambulacra with three acuminate lobes. Setae of legs II–IV mainly stout and arising from conspicuous protuberances.

MALE. Unknown.

LOCALITIES. Uganda and Sudan. The holotype female (1959.1.20.112) from rushes and grassland bordering hot springs, sixteen miles east-north-east of Bundibugyo, Ruwenzori, Uganda, 29.viii.1952, collected by G. O. Evans; and two paratype females (1959.1.20.113–114) on *Papyrus* in the Sudd Region, Southern Sudan, collected by I. W. B. Thornton.

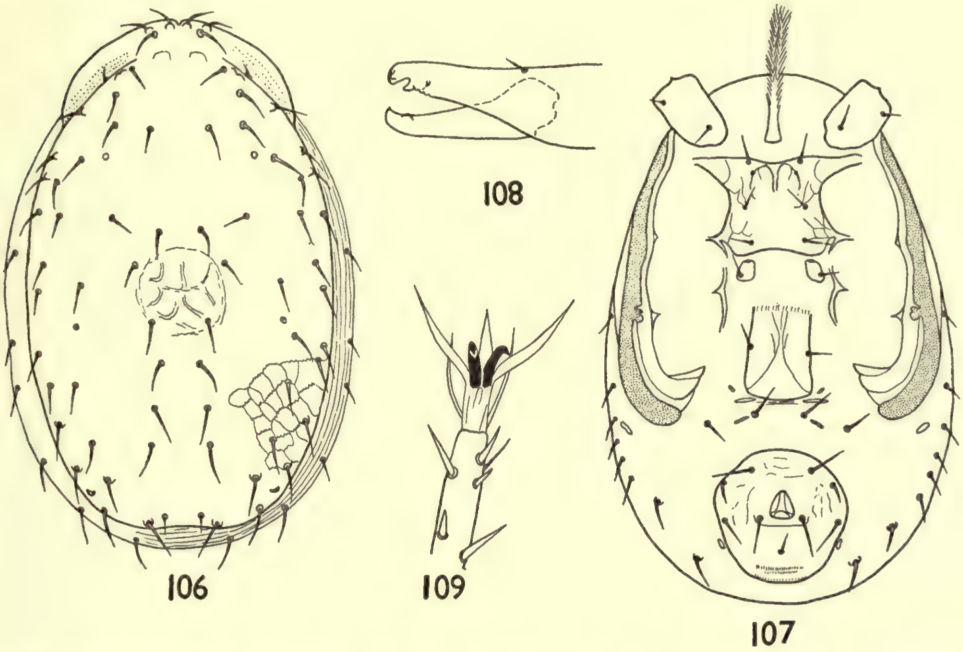


FIGS. 103–105. *Sejus spinipes* sp. nov., female. Fig. 103, dorsal shield. Fig. 104, venter. Fig. 105, chelicera.

Sejus nepalensis sp. nov.

FEMALE. Dorsal shield (456–498 μ long × 289–299 μ wide) completely covered by a fine reticulated pattern (Text-fig. 106). " Anterior dorsal shield " with twenty-one pairs of simple setae ; vertical setae relatively short and directed laterally ; vertex not well developed. " Posterior dorsal shield " with fifteen pairs of simple setae (in the holotype seta Z1 is missing from the left side) ; seta J5 is the shortest. All dorsal setae arise from small tubercles. The distribution and relative lengths of the setae and the ornamentation of the dorsal shield are shown in the Text-fig.

Tritosternum well developed, with pilose laciniae, sternal shield with some sculpturing, a pair of circular areas anteriorly, and bearing three pairs of simple setae (Text-fig. 107). Genital shield almost parallel sided and bearing one pair of simple setae. Ventri-anal shield (126 μ long × 124–127 μ wide) almost circular in outline, bearing nine simple setae ; anus more or less central. Between the genital and ventri-anal shields lie about four narrow platelets. Stigma situated between coxae III and IV ; peritreme extending posterior to coxa IV. Metapodal plates very small.



FIGS. 106–109. *Sejus nepalensis* sp. nov., female. Fig. 106, dorsum. Fig. 107, venter. Fig. 108, chelicera. Fig. 109, tarsus II.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum three-pronged and typical of the genus. The dentition of the chelicera is shown in Text-fig. 108.

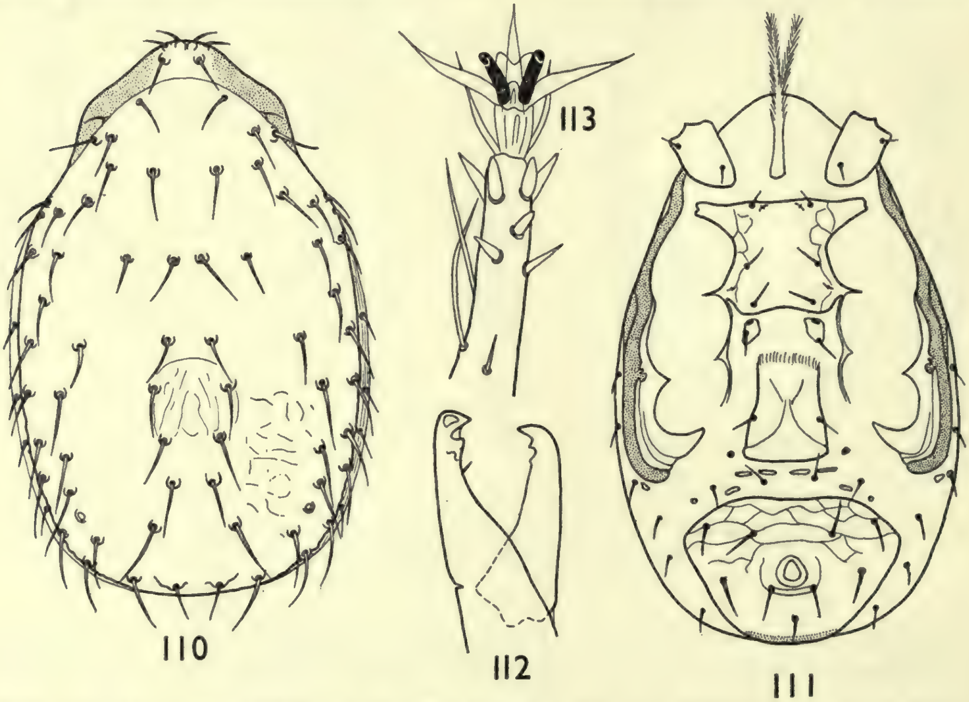
Leg I (630–769 μ long) with the tarsus (126–157 μ) shorter than the tibia (150–195 μ). Setae on tarsus, tibia and genu very fine; those on remaining segments stouter. Claws very small, pulvillus short. Tarsi II–IV with a pair of lanceolate setae; ambulacra with three acuminate lobes (Text-fig. 109).

MALE. Unknown.

LOCALITY. Nepal. The holotype female (1959.1.20.115) from sandy turf on open grazed hillside facing south at Siklis (28° 22′ N., 84° 6′ E.), 7,000 ft., 20–21.iv.1954; and one paratype female (1959.1.20.116) from damp mossy and grassy earth under shade of trees and rocks at Bakhri Kharka (28° 22·5′ N., 84° 7·5′ E.), 5,500 ft., 24.iv.1954, collected by K. H. Hyatt.

Sejus parbatensis sp. nov.

FEMALE. Dorsal shield (402–435 μ long × 237–268 μ wide) covered by an irregular reticulated pattern (Text-fig. 110). "Anterior dorsal shield" with twenty-one pairs of simple setae; verticals with their bases contiguous. "Posterior dorsal shield" with fifteen pairs of simple setae; setae J5 are more than half the length of J4. All the setae arise from small tubercles. The distribution of the setae, and the ornamentation of the dorsal shield are shown in the Text-fig.



FIGS. 110–113. *Sejus parbatensis* sp. nov., female. Fig. 110, dorsum. Fig. 111, venter. Fig. 112, chelicera. Fig. 113, tarsus II.

Tritosternum well developed and with pilose laciniae. Sternal shield lightly sculptured and bearing three pairs of simple setae (Text-fig. 111). Genital shield bearing a single pair of setae. Ventri-anal shield wider than long (114–126 μ long × 157–170 μ wide), reticulated, and bearing nine simple setae. Between the genital and ventri-anal shields lies a row of four narrow platelets, and, posterior to these, two smaller ones. Stigma situated between coxae III and IV; peritreme extending posterior to coxa IV. Metapodal plates very small.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum three-pronged and typical of the genus. The dentition of the chelicera is shown in Text-fig. 112.

Leg I (c. 340 μ long) with the tarsus (80–83 μ) longer than the tibia (50–53 μ). Setae on tarsus I very fine; those on remaining segments stouter; claws small, on short pulvillus. Tarsi II–IV with a pair of lanceolate setae; ambulacra with three acuminate lobes (Text-fig. 113).

MALE. Unknown.

LOCALITY. Nepal. The holotype female (1959.1.20.117) and one paratype (1959.1.20.118) from litter under a group of deciduous trees forming a canopy on open ground at Gurjakhani (28° 36·5′ N., 83° 13·5′ E.) on the southern slope of the Dhaulagiri Himal, 8,500 ft., 24–27.vi.1954; and one paratype female (1959.1.20.119) in sandy turf on open, grazed hillside facing south at Siklis (28° 22′ N., 84° 6′ E.), 7,000 ft., 20–21.iv.1954, collected by K. H. Hyatt.

Sejus clayi sp. nov.

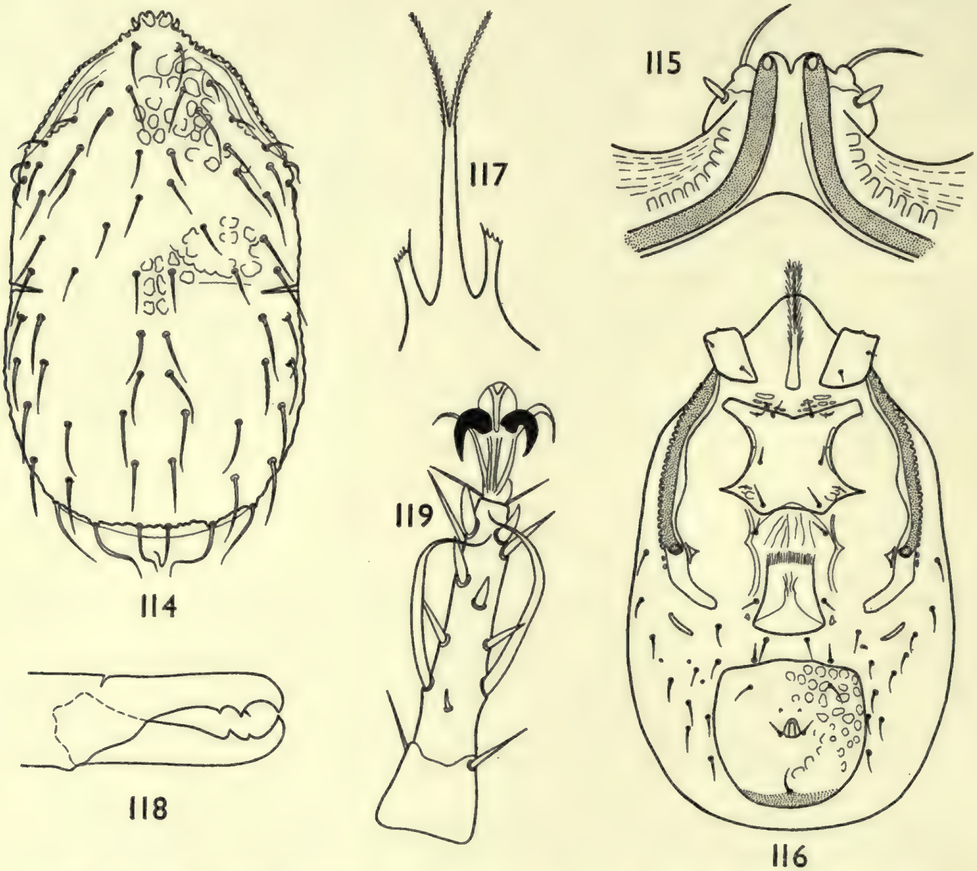
FEMALE. Dorsal shield (661 μ long × 366 μ wide) with lateral incisions anterior to S1, and heavily marked with circular depressions (Text-fig. 114). Vertex of dorsal shield produced anteriorly (Text-fig. 115). "Anterior dorsal shield" with twenty pairs of setae; verticals absent, para-verticals short and spatulate, remaining setae simple. "Posterior dorsal shield" with fifteen pairs of simple setae. Setae J5 are long. The distribution and relative lengths of the dorsal setae are shown in Text-fig. 114.

Tritosternum well developed with pilose laciniae and flanked at its base by a number of fragmented pre-endopodal shields. Sternal shield plain and bearing three pairs of simple setae (Text-fig. 116). Genital shield wedge shaped, genital setae off the shield. Ventri-anal shield slightly wider than long (185 μ long × 190 μ wide), covered with small circular depressions, and bearing only five simple setae. Stigma situated between coxae III and IV, peritreme not extending posterior to the stigma; external margin of peritreme strongly crenate. Peritrematal shield extending posterior to coxa IV. Metapodal shields narrow and obliquely situated.

Venter of the gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on legs simple. Tectum (Text-fig. 117) differing from that of other members of the genus in that the median prong is strongly produced and terminates in a pair of pilose laciniae. The dentition of the chelicera is shown in Text-fig. 118.

Leg I (481 μ long) with the tarsus (126 μ) longer than the tibia (101 μ). Setae on tarsus I very fine; those on remaining segments stouter. Tarsi II–IV with a pair of lanceolate setae and ambulacra with lateral lobes acuminate, median lobe short and rounded (Text-fig. 119). Ambulacrum of tarsus I short with claws very small.

MALE. Unknown.

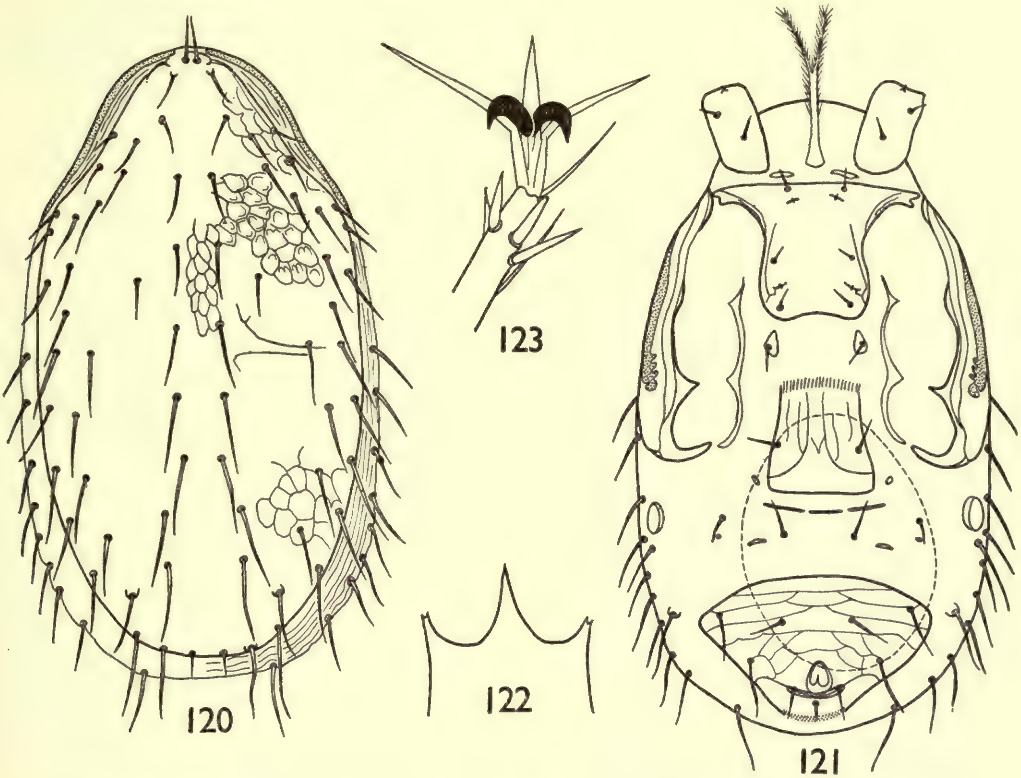


FIGS. 114–119. *Sejus clayi* sp. nov., female. Fig. 114, dorsum. Fig. 115, vertex. Fig. 116, venter. Fig. 117, tectum. Fig. 118, chelicera. Fig. 119, tarsus II.

LOCALITY. Sikkim. A single female (1959.1.20.120) from leaves and leaf-mould in wood on steep hillside, Chungtang, 5,120 ft., 16.ii.1952, collected by Dr. Theresa Clay.

Sejus alstoni sp. nov.

FEMALE. Dorsal shield (507–550 μ long × 279–340 μ wide) covered anteriorly by a network of small depressions and ridges, and posteriorly by a reticulated pattern (Text-fig. 120). "Anterior dorsal shield" with twenty-one pairs of simple setae; verticals close together and directed anteriorly. "Posterior dorsal shield" with fifteen pairs of simple setae, of which J5 are the shortest. The distribution and relative lengths of the dorsal setae, and the ornamentation of the dorsal shield are shown in the Text-fig.



FIGS. 120–123. *Sejus alstoni* sp. nov., female. Fig. 120, dorsum. Fig. 121, venter. Fig. 122, tectum. Fig. 123, tarsus II.

Tritosternum well developed with pilose laciniae, and flanked at its base by a pair of narrow pre-endopodal shields. Sternal shield weakly sclerotized, without ornamentation, and bearing three pairs of simple setae (Text-fig. 121). Genital shield truncated posteriorly and bearing one pair of setae. Ventri-anal shield broader than long (139–152 μ long × 180–205 μ wide), reticulated, and bearing nine simple setae. Between the genital and ventri-anal shields lies a row of three narrow sclerotized plates. Stigma situated between coxae III and IV; no posterior prolongation of the peritreme. Peritrematal shield extending posterior to coxa IV. Metapodal shields elliptical.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum (Text-fig. 122) three-pronged and typical of the genus. Chelicerae typical.

Leg I (560–565 μ long) with the tarsus (160 μ) one-and-a-half times as long as the tibia (101–104 μ). Setae on tarsus fine ; claws small ; setae on remaining segments stouter. Tarsi II–IV with a pair of lanceolate setae and ambulacra with three acuminate lobes (Text-fig. 123).

MALE. Unknown.

LOCALITY. Indonesia. The holotype female (1959.1.20.121) and two paratype females (1959.1.20.122–123) in decaying vegetation at Bogor, 1954, collected by the late A. H. G. Alston.

Sejus aciculatus sp. nov.

FEMALE. Dorsal shield (329–341 μ long × 223–231 μ wide) very heavily sclerotized, entirely covered by a network of ridges and depressions (Text-fig. 124). " Anterior dorsal shield " with nineteen pairs of simple setae, verticals and paraverticals apparently absent. " Posterior dorsal shield " with fifteen pairs of simple setae. The distribution and relative lengths of the dorsal setae, and the characteristic ornamentation of the dorsal shield are shown in the Text-fig.

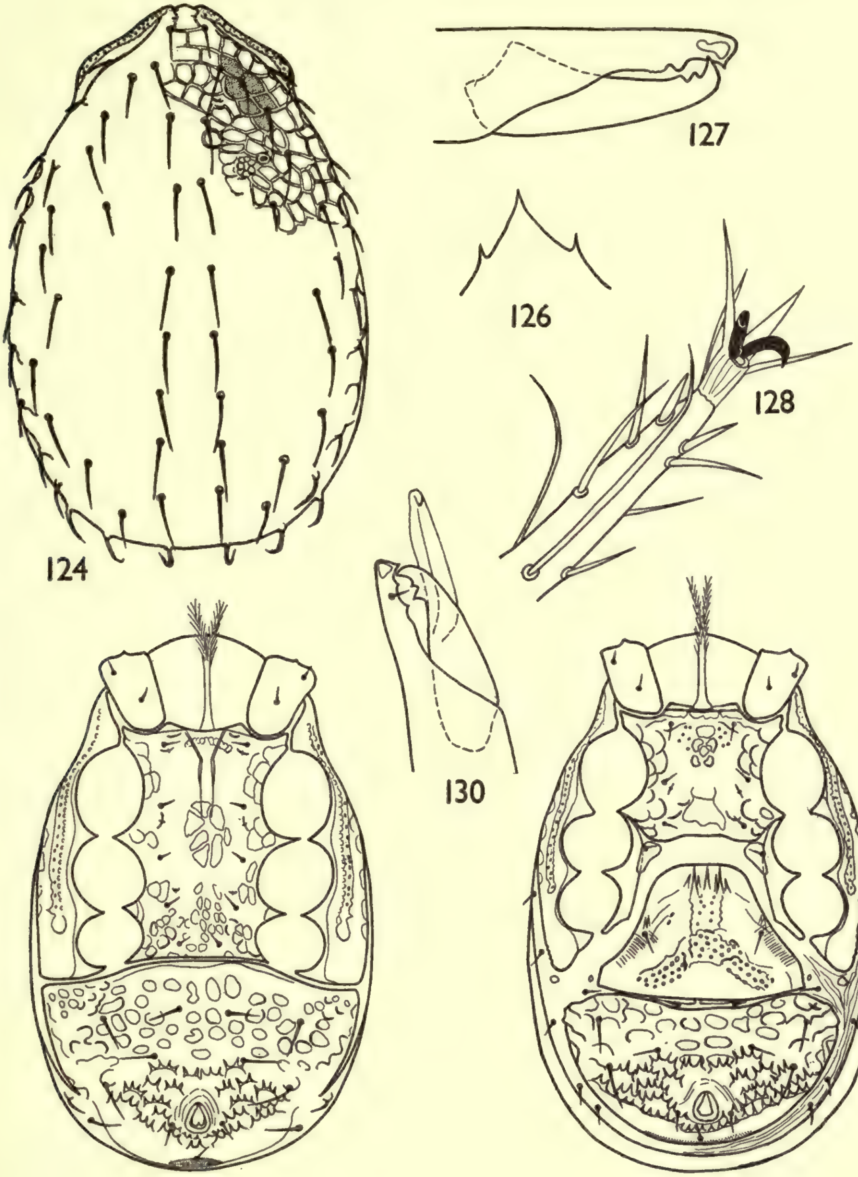
Tritosternum well developed and flanked at its base by a pair of strong preendopodal shields which abut the sternal shield. Sternal shield characteristically ornate (Text-fig. 125) and bearing three pairs of simple setae. Genital shield approximately in the form of a trapezium, heavily sclerotized and ornate, and bearing a single pair of simple setae. Ventri-anal shield broader than long (88–96 μ long × 172–180 μ wide), concave anteriorly, strongly ornate, and bearing nine simple setae. Between the genital and ventri-anal shields lies a pair of narrow sclerotized platelets. Stigma situated between coxae III and IV and peritreme not extending posterior to the stigma. Peritrematal shield well developed and extending posterior to coxa IV. Metapodal plates small.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whiplike. All setae on pedipalp simple. Tectum (Text-fig. 126) three-pronged, median prong broad and triangular, lateral prongs small, inconspicuous. Dentition of chelicera as in Text-fig. 127.

Leg I (245–255 μ long) with the tarsus (88–94 μ) twice the length of the tibia (43–45 μ). Setae on tarsus I very fine, ambulacrum short, claws small. Setae of remaining segments stouter. Tarsi II–IV with a pair of lanceolate setae, and ambulacra with three acuminate lobes (Text-fig. 128).

MALE. Dorsal shield (276–283 μ long × 180–185 μ wide) with ornamentation and chaetotaxy similar to the female.

Tritosternum of the same form as that of the female. The chaetotaxy and sclerotization of the venter are shown in Text-fig. 129. The gnathosoma and tectum are similar to those of the female. The spermatophoral process is about the same length as the movable digit of the chelicera (Text-fig. 130).



FIGS. 124–130. *Sejus aciculatus* sp. nov. Fig., 124 dorsal shield of female. Fig. 125, venter of female. Fig. 126, tectum of female. Fig. 127, chelicera of female. Fig. 128, tarsus II of female. Fig. 129, venter of male. Fig. 130, chelicera of male.

Leg I (281 μ long) with the tarsus (81 μ) twice the length of the tibia (38 μ). The chaetotaxy and ambulacra of the legs are as in the female.

LOCALITY. Jamaica, B.W.I. The holotype female (1959.1.20.124), allotype male (1959.1.20.125), seven female and three male paratypes (1959.1.20.126–133) from damp leaf litter at St. Ann, Mt. Diablo, 1,500 ft. and 2,200 ft., 3.vi.1956, collected by P. F. Bellinger. A male and female paratype have been returned to the collector.

Sejus antillanus sp. nov.

FEMALE. Dorsal shield (333–443 μ long × 195–278 μ wide) slightly attenuated in its posterior half, and entirely covered by a reticulated pattern (Text-fig. 131). " Anterior dorsal shield " with twenty-one pairs of simple setae, verticals almost contiguous and directed anteriorly. " Posterior dorsal shield " with fifteen pairs of simple setae ; J5 are the shortest. The distribution and relative lengths of the setae, and the ornamentation of the dorsal shield are shown in the Text-fig.

Tritosternum well developed with pilose laciniae. Sternal shield with a reticulated area anteriorly and bearing three pairs of simple setae (Text-fig. 132). Genital shield truncated posteriorly, reticulated, and bearing a single pair of setae. Ventri-anal shield broader than long (76–101 μ long × 101–114 μ wide), reticulated, with nine simple setae of which one pair is long. Between the genital and ventri-anal shields lies a row of four small narrow sclerotized plates, and behind these a pair of smaller plates. Stigma situated between coxae III and IV ; no post-stigmal prolongation of the peritreme. Peritrematal shield extending posterior to coxae IV. Metapodal shields small.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum (Text-fig. 133) three-pronged. The dentition of the chelicera is shown in Text-fig. 134.

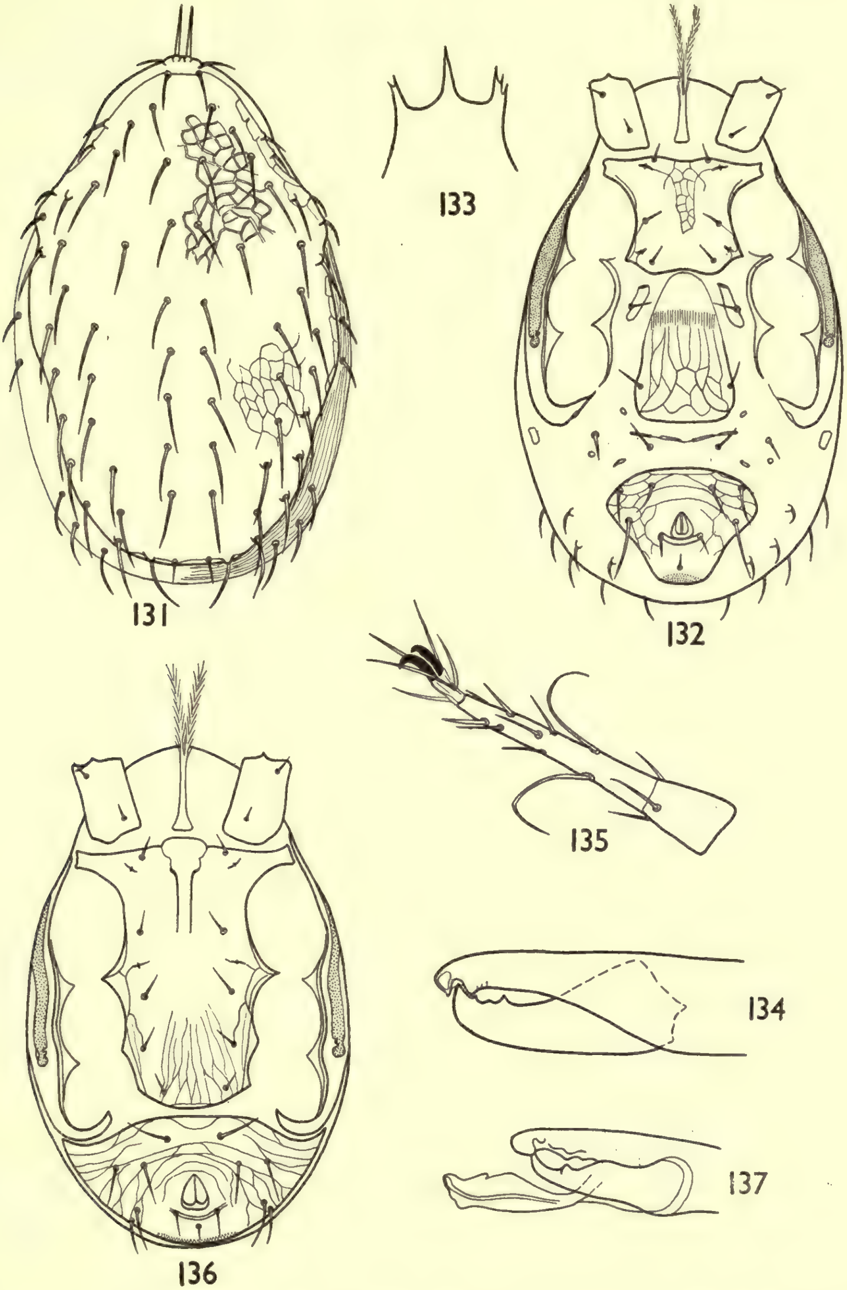
Leg I (384–521 μ long) with the tarsus (86–139 μ) slightly longer than the tibia (78–114 μ). Setae on tarsus and tibia fine, those on remaining segments stouter ; claws on leg I small. Tarsi II–IV with a pair of lanceolate setae and ambulacra with acuminate lobes (Text-fig. 135). Leg IV (532–797 μ) considerably longer than the idiosoma, with the tarsus 203–316 μ long.

MALE. Dorsal shield (236–303 μ long × 147–203 μ wide) having similar chaetotaxy and ornamentation to the female.

The chaetotaxy and sclerotization of the venter are shown in Text-fig. 136. The gnathosoma and tectum are similar to those of the female. The spermatophoral process is about one-and-a-half times the length of the movable digit (Text-fig. 137).

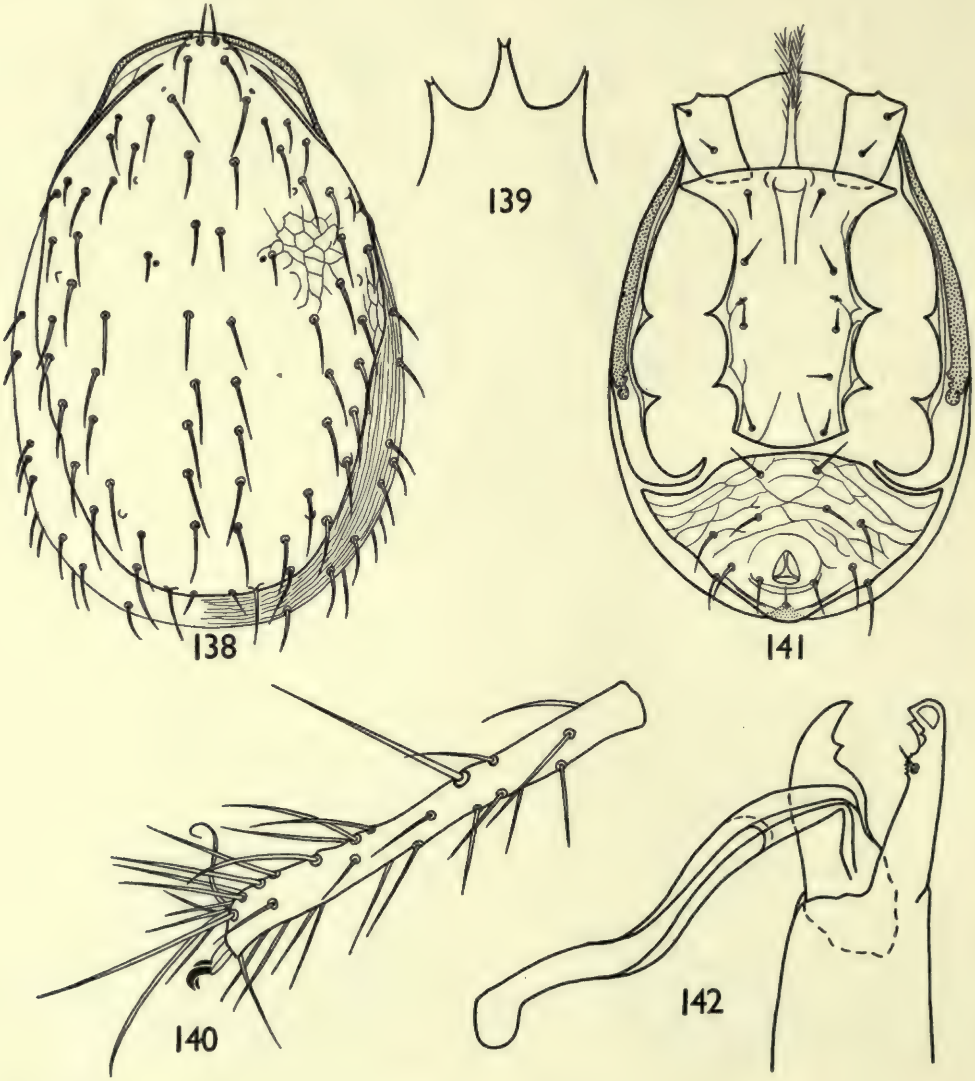
Leg I (238–432 μ long) with the tarsus (76–116 μ) longer than the tibia (63–88 μ). Leg IV (448–658 μ long) with the tarsus 170–253 μ. The chaetotaxy and ambulacra of the legs are as in the female.

LOCALITY. Jamaica, B.W.I. The holotype female (1959.1.20.134) and four paratype females (1959.1.20.135–138) from damp leaf litter, Mt. Diablo, St. Ann, 2,200 ft., 7.vi.1956 ; the allotype male (1959.1.20.139) and five paratypes (3♂♂,



FIGS. 131–137. *Sejus antillanus* sp. nov. Fig. 131, dorsum of female. Fig. 132, venter of female. Fig. 133, tectum of female. Fig. 134, chelicera of female. Fig. 135, tarsus II of female. Fig. 136, venter of male. Fig. 137, chelicera of male.

2♀♀) (1959.1.20.140–144) from damp leaf litter in wood, Dolphin Head, Hanover, 1,780 ft., 13.iv.1956; three paratypes (1♂, 2♀♀) in moss, St. Thomas, John Cove Mountains, 2,300 ft., 25.v.1956; and ten paratypes (1♂, 9♀♀) (1959.1.20.145–154) from leaf litter, Portland Gap, 8.iii.1956. All were collected by P. F. Bellinger. A male and two female paratypes have been returned to the collector.



Figs. 138–142. *Sejus bellingeri* sp. nov. Fig. 138, dorsum of female. Fig. 139, tectum of female. Fig. 140, tarsus I of female. Fig. 141, venter of male. Fig. 142, chelicera of male.

Sejus bellingeri sp. nov.

FEMALE. Dorsal shield (467–507 μ long × 299–310 μ wide) slightly attenuated in its posterior half, and covered by a reticulated pattern (Text-fig. 138). " Anterior dorsal shield " with twenty-one pairs of simple setae ; verticals closely situated and directed anteriorly. " Posterior dorsal shield " with fifteen pairs of simple setae of which J5 are the shortest. The distribution and relative lengths of the setae and the ornamentation of the dorsal shield are shown in the Text-fig.

The chaetotaxy and sclerotization of the venter are essentially the same as in *Sejus nodosus* (p. 85). The ventri-anal shield measures 119–139 μ long × 132–156 μ wide.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum (Text-fig. 139) three-pronged, and chelicerae typical of the genus.

Leg I (c. 589 μ long) with the tarsus (c. 157 μ) longer than the tibia (c. 126 μ). Tarsus I with a strong erect seta dorsally (Text-fig. 140), remaining setae fine ; tarsal claws small but conspicuous. Tarsi II–III with a pair of lanceolate setae (tarsus IV has only one such seta), ambulacra with three acuminate lobes. Leg IV (c. 913 μ) longer than the idiosoma. Tarsus IV (303–341 μ) markedly elongate and three times the length of the tibia.

MALE. Dorsal shield (347 μ long × 228 μ wide) not attenuated in its posterior half, lightly reticulated. The chaetotaxy of the dorsal shield is the same as that of the female.

The chaetotaxy and ornamentation of the venter are shown in Text-fig. 141. The gnathosoma and tectum are similar to those of the female. Spermatophoral process about twice the length of the movable digit of the chelicera (Text-fig. 142).

Leg I (481 μ long) with the tarsus (126 μ) longer than the tibia (99 μ). Tarsus I with a strong erect seta dorsally as in the female. Leg IV (675 μ long) longer than the idiosoma, and with the tarsus (265 μ) three times the length of the tibia (88 μ).

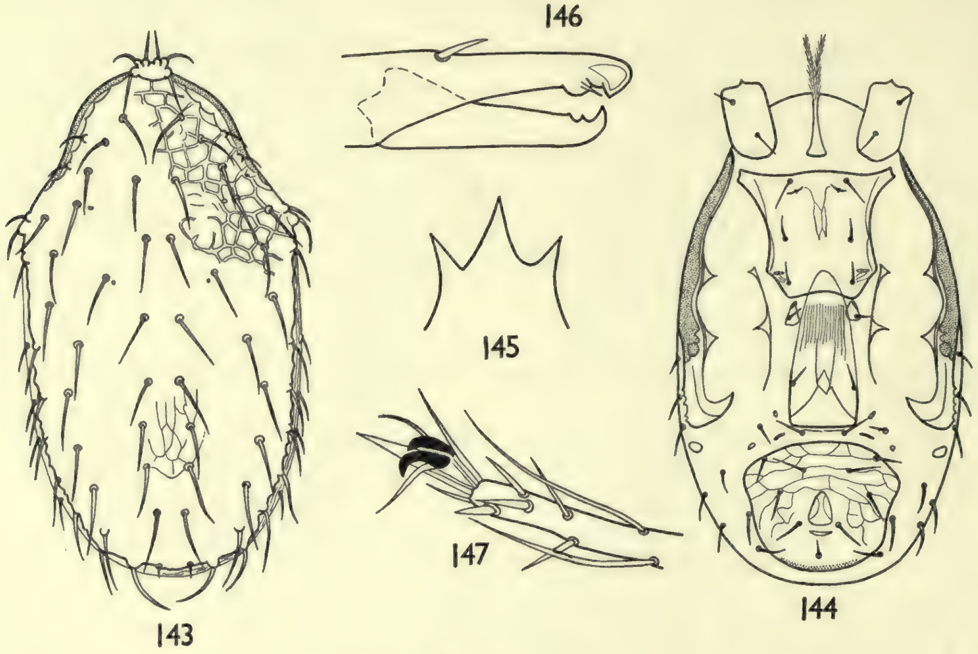
LOCALITY. Jamaica, B.W.I. The holotype female (1959.1.20.155), allotype male (1959.1.20.156) and one paratype female from pine and hardwood litter, St. Thomas, Portland Gap, 5,500 ft., 8.iii.1956, collected by P. F. Bellinger. The paratype has been returned to the collector.

Sejus hulli sp. nov.

FEMALE. Dorsal shield (359 μ long × 195 μ wide) completely covered by a conspicuous reticulated pattern (Text-fig. 143). " Anterior dorsal shield " with twenty-one pairs of simple setae, verticals on a prominent protuberance and directed anteriorly. " Posterior dorsal shield " with fifteen pairs of simple setae, J5 are short. All setae arise from small protuberances. The distribution and relative lengths of the dorsal setae and the ornamentation of the dorsal shield are shown in the Text-fig.

Tritosternum well developed with pilose laciniae. Sternal shield with a very faint reticulated area medially, and bearing three pairs of simple setae (Text-fig. 144). Genital shield bearing a single pair of setae. Ventri-anal shield a little broader than long (94 μ long × 114 μ wide), reticulated and bearing nine simple setae. Between the genital and ventri-anal shields lie about six small sclerotized plates. Stigma situated between coxae III and IV; no distinct post-stigmal prolongation of peritreme; peritrematal shield extending posterior to coxa IV. Metapodal plates small.

Venter of gnathosoma with rostral and internal seta on palptrochanter long, whip-like. All setae on pedipalp simple. Tectum (Text-fig. 145) three-pronged. The dentition of the chelicera is shown in Text-fig. 146.



Figs. 143–147. *Sejus hulli* sp. nov., female. Fig. 143, dorsum. Fig. 144, venter. Fig. 145, tectum. Fig. 146, chelicera. Fig. 147 tarsus II.

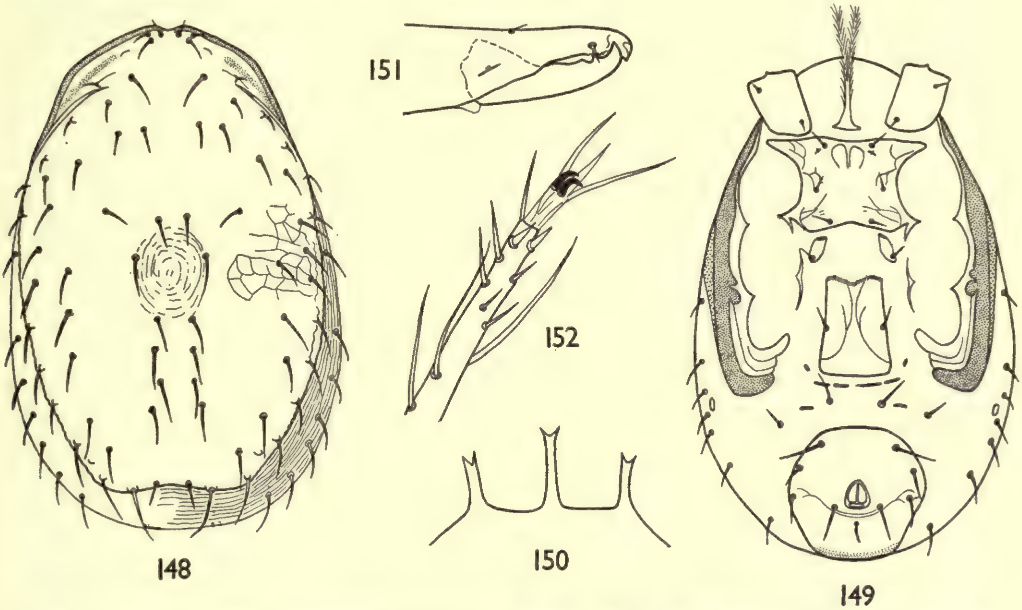
Leg I (360 μ) with the tarsus (101 μ) nearly twice the length of the tibia (56 μ). Setae on tarsus and tibia fine, those on remaining segments stouter. Claws on leg I minute, tarsus swollen in its distal third. Tarsi II–IV with a pair of lanceolate setae, and ambulacra with acuminate lobes (Text-fig. 147).

Male. Unknown.

Locality. Jamaica, B.W.I. A single female (1959.1.20.157) collected in *Lycopodium* at Fairy Glade, St. Andrew, 6.xii.1956, by P. F. Bellinger.

Sejus jamaicensis sp. nov.

FEMALE. Dorsal shield (477 μ long × 310 μ wide) concave posteriorly and covered with a light reticulated pattern (Text-fig. 148). " Anterior dorsal shield " with twenty-one pairs of simple setae ; verticals well separated, short, and arising from weak bases. " Posterior dorsal shield " with fifteen pairs of simple setae of which J5 are the shortest. The distribution of the dorsal setae and the ornamentation of the dorsal shield are shown in the Text-fig.



FIGS. 148–152. *Sejus jamaicensis* sp. nov., female. Fig. 148, dorsum. Fig. 149, venter. Fig. 150 tectum. Fig. 151, chelicera. Fig. 152, tarsus II.

Tritosternum well developed with pilose laciniae. Sternal shield with a little sculpturing and two circular areas anteriorly (Text-fig. 149), and bearing three pairs of simple setae. Genital shield with one pair of simple setae. Ventri-anal shield wider than long (114–119 μ long × 139–144 μ wide), bearing nine simple setae, and only lightly sculptured. Between the genital and ventri-anal shields lie a row of four narrow platelets and, posterior to these, two smaller ones. Stigma situated between coxae III and IV ; peritreme extending posterior to coxa IV. Metapodal plates very small.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum (Text-fig. 150) three-pronged. The dentition of the chelicera is shown in Text-fig. 151.

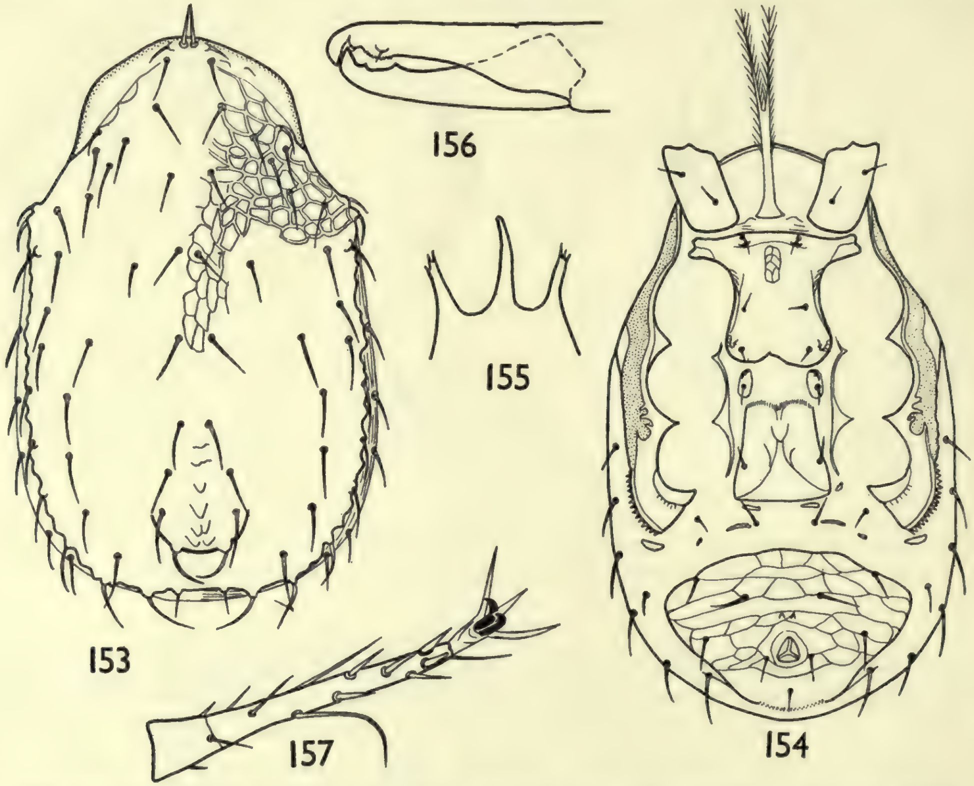
Leg I (924 μ long) with the tarsus (215 μ) only slightly shorter than the tibia (228 μ). Setae on tarsus, tibia and genu very fine ; those on remaining segments stouter. Claws minute, sessile. Tarsi II–IV with a pair of lanceolate setae; ambulacra with three acuminate lobes (Text-fig. 152).

MALE. Unknown.

LOCALITY. Jamaica, B.W.I. The holotype female (1959.1.20.158) and one paratype female from wet leaves in spray zone, Cape Crow Falls, St. Andrew, 31.iii.1956, collected by P. F. Bellinger. The paratype has been returned to the collector.

Sejus neborealis sp. nov.

FEMALE. Dorsal shield (570 μ long × 330–340 μ wide) entirely covered by a strong reticulated pattern, and with a sclerotized tubercle in the region of setae J3–J4 (Text-fig. 153). " Anterior dorsal shield " with twenty-one pairs of simple setae, vertical setae contiguous and directed anteriorly. "Posterior dorsal shield" with fifteen pairs of simple setae, J4 situated on the margin of the sclerotized tubercle. The distribution and relative lengths of the dorsal setae, and the ornamentation of the dorsal shield are shown in the Text-fig.



FIGS. 153–157. *Sejus neborealis* sp. nov., female. Fig. 153, dorsum. Fig. 154, venter. Fig. 155, tectum. Fig. 156, chelicera. Fig. 157, tarsus II.

Tritosternum well developed with pilose laciniae. Sternal shield with a small median reticulated area anteriorly, and bearing three pairs of short simple setae (Text-fig. 154). Genital shield slightly convex posteriorly and bearing one pair of simple setae. Ventri-anal shield broader than long (172–177 μ long × 240–253 μ wide), wholly reticulated and bearing nine simple setae. Between the genital and ventri-anal shields lie four sclerotized platelets. Stigma situated between coxae III and IV with the posterior prolongation of the peritreme extending in line with the middle of coxa IV. Peritrematal shield well developed, extending posterior to coxa IV, and crenate externally. Metapodal plates small.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum (Text-fig. 155) three-pronged. The dentition of the chelicera is shown in Text-fig. 156.

Leg I (734–774 μ long) with the tarsus (228–243 μ) approximately twice the length of the tibia (114–126 μ). Some setae on tarsus I relatively long and standing at right angles to the segment ; ambulacrum short, claws small (and inconspicuous) ; setae of remaining segments stouter. Tarsi II–IV with a pair of lanceolate setae and ambulacrum with three acuminate lobes (Text-fig. 157).

MALE. Unknown.

LOCALITY. Jamaica, B.W.I. The holotype female (1959.1.20.158) and three paratype females (1959.1.20.159–160) collected in moss on concrete, Coolsbade, Portland, 17.vii.1956, by P. F. Bellinger. One paratype has been returned to the collector.

Sejus nodosus sp. nov.

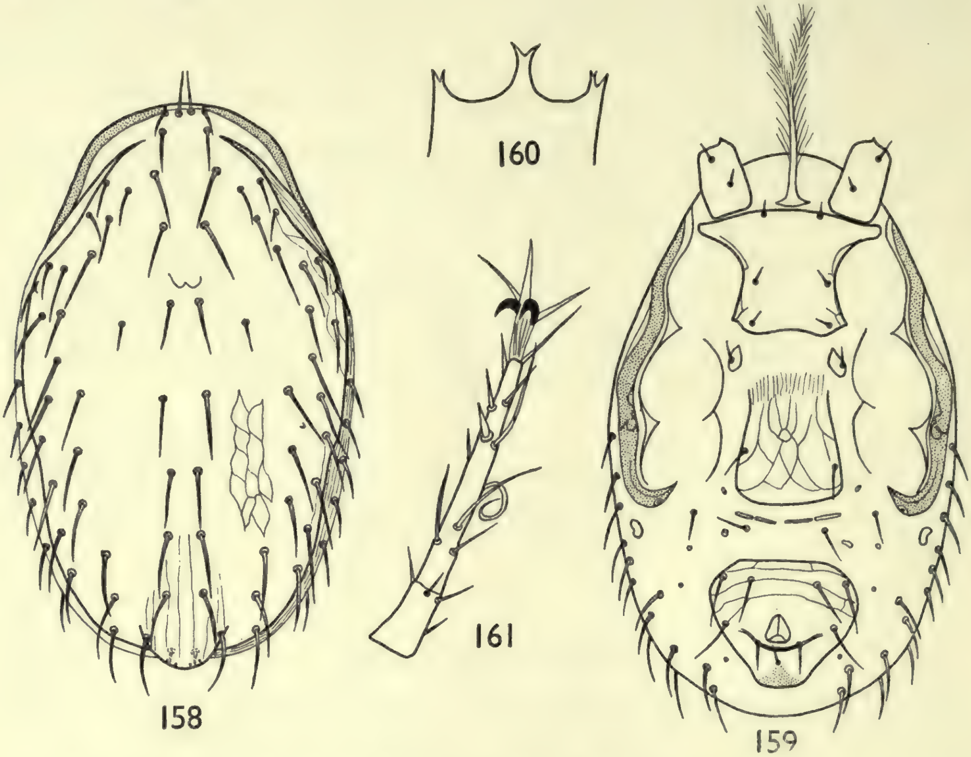
FEMALE. Dorsal shield (518–529 μ long × 310 μ wide) slightly attenuated in its posterior half, and covered by a reticulated pattern (Text-fig. 158). There is a pronounced sclerotized tubercle in the region of setae J3–J4. " Anterior dorsal shield " with twenty-one pairs of simple setae ; vertical setae closely situated and anteriorly directed. " Posterior dorsal shield " with twenty-one pairs of simple setae, of which J5 are the shortest. The distribution and relative lengths of the setae and the ornamentation of the dorsal shield are shown in the Text-fig.

Tritosternum well developed and with pilose laciniae. Sternal shield plain and bearing three pairs of simple setae (Text-fig. 159). Genital shield slightly convex posteriorly, reticulated, and bearing a single pair of setae. Ventri-anal shield wider than long (114–116 μ long × 134–144 μ wide), lightly sculptured and bearing nine simple setae. Between the genital and ventri-anal shields lies a row of two to four narrow sclerotized platelets. Stigma situated between coxae III and IV ; peritreme not extending posterior to the stigma. Metapodal plates small.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum (Text-fig. 160) three-pronged, and chelicerae typical of the genus.

Leg I (c. 620 μ long) with the tarsus (165 μ) longer than the tibia (126 μ). Tarsus I with a strong erect spine dorsally, remaining setae fine ; tarsal claws small but conspicuous. Tarsi II–III with a pair of acuminate lobes (Text-fig. 161.) Leg IV is about 913 μ long, with the tarsus 392 μ long, markedly elongate, and three times as long as the tibia.

MALE. Unknown.



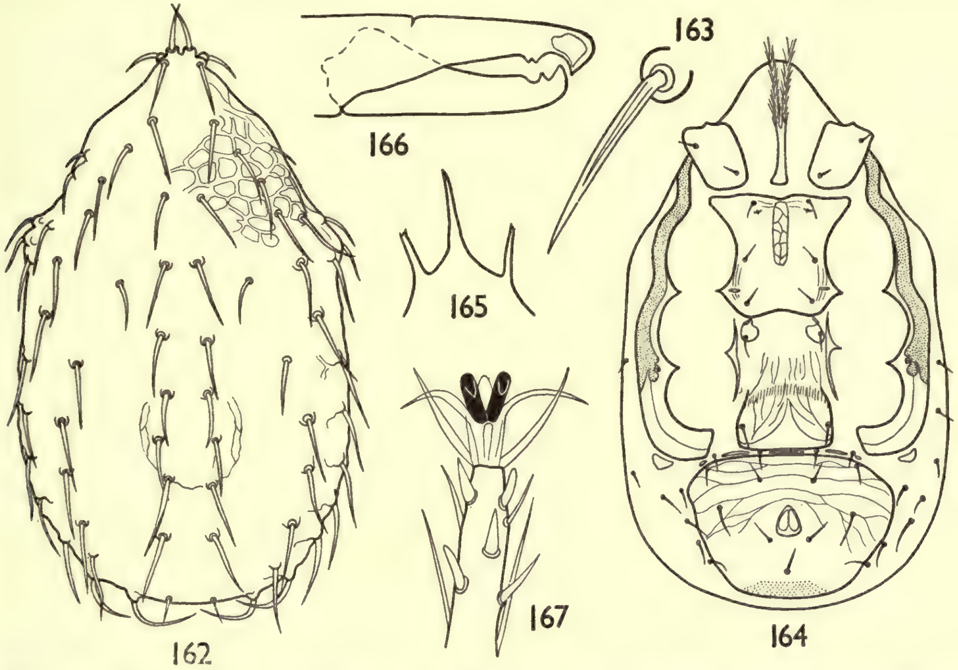
FIGS. 158–161. *Sejus nodosus* sp. nov., female. Fig. 158, dorsum. Fig. 159, venter. Fig. 160, tectum. Fig. 161, tarsus II.

LOCALITY. Jamaica, B.W.I. The holotype female (1959.1.20.161) and one paratype from moss on concrete, Coolsbade, Portland, 17.vii.1955, collected by P. F. Bellinger. The paratype has been returned to the collector.

Sejus browningi sp. nov.

FEMALE. Dorsal shield (330–354 μ long × 190–210 μ wide) very heavily reticulated (Text-fig. 162). "Anterior dorsal shield" with twenty-one pairs of setae; "posterior dorsal shield" with fifteen pairs of setae. Dorsal setae J5 are short and simple, but the remainder are lanceolate (Text-fig. 163). The highest part of the dorsal shield is in the region of setae J1–J3. The vertex is produced anteriorly. The distribution and relative lengths of the dorsal setae are shown in Text-fig. 162.

Tritosternum with a pair of pilose laciniae. Sternal shield with a narrow longitudinal reticulated area anteriorly (Text-fig. 164) and bearing three pairs of simple setae. Genital shield broad, truncated posteriorly, lightly striated and bearing a single pair of simple setae. Ventri-anal shield wider than long (99–101 μ long × 121–139 μ wide), lightly reticulated anteriorly, and bearing nine simple setae. A row of five narrow sclerotized plates lies on the membrane between the genital and ventri-anal shields. Stigma situated between coxae III and IV, with the peritreme extending only a short distance posterior to the stigma. Peritrematal shield extending posterior to coxa IV. Metapodal shields triangular and situated close to the peritrematal shield.



Figs. 162–167. *Sejus browningi* sp. nov., female. Fig. 162, dorsal shield. Fig. 163, dorsal seta. Fig. 164, venter. Fig. 165, tectum. Fig. 166, chelicera. Fig. 167, tarsus II.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum (Text-fig. 165) three-pronged and typical of the genus. The dentition of the chelicera is shown in Text-fig. 166.

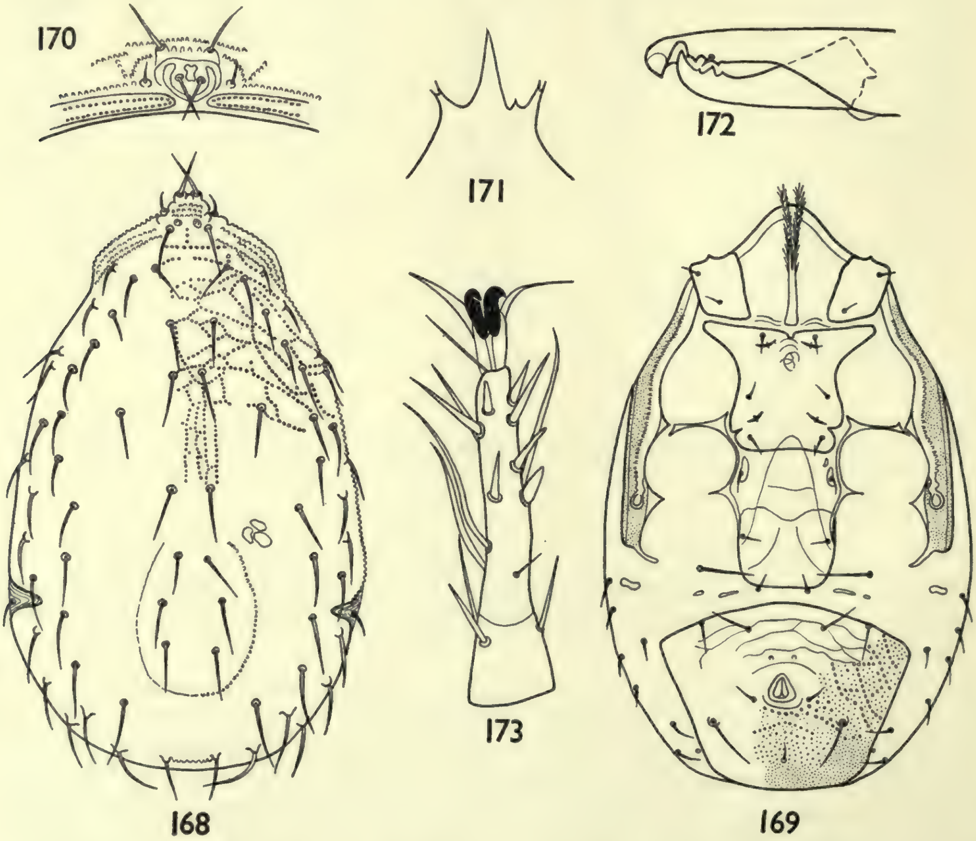
Leg I (320–340 μ long) with the tarsus (88 μ) longer than the tibia (58 μ). Setae on tarsus I very fine; those on remaining segments somewhat stouter. Tarsus I is swollen in its distal third; without ambulacrum. Tarsi II–IV with a pair of lanceolate setae, and ambulacra with lateral lobes acuminate; median lobe strongly produced and rounded apically (Text-fig. 167).

MALE. Unknown.

LOCALITY. Sikkim and Argentina. The holotype female (1959.1.20.162) and two paratype females (1959.1.20.163–164) from leaves and leaf-mould in a wood on steep hillside, Chungtang, Sikkim, 5,120 ft., 16.ii.1952, collected by Dr. Theresa Clay; and another paratype female (1959.1.20.165) from rotting vegetable matter, Tucumán City, Argentina, 500 m., January, 1953, collected by Dr. P. Wygodzynsky.

Sejus ornatus sp. nov.

FEMALE. Dorsal shield (395–400 μ long × 245–253 μ wide) with lateral incisions between setae S2 and S3, and covered by a network of small tubercles (Text-fig. 168). Highest part of dorsal shield in the region of setae J1–J3. "Anterior dorsal shield" with twenty-two pairs of simple setae; "posterior dorsal shield" with fifteen pairs of simple setae. Setae J5 are long. Vertex of dorsal shield produced ante-



FIGS. 168–173. *Sejus ornatus* sp. nov., female. Fig. 168, dorsum. Fig. 169, venter. Fig. 170, vertex. Fig. 171, tectum. Fig. 172, chelicera. Fig. 173, tarsus II.

riorly. The distribution and relative lengths of the dorsal setae and the ornamentation of the dorsal shield are shown in the Text-fig.

Tritosternum well developed, with pilose laciniae. Sternal shield with a circular impression antero-medially and bearing three pairs of simple setae (Text-fig. 169). Genital shield broad, truncated posteriorly, and bearing a single pair of setae. Ventri-anal shield wider than long (118–139 μ long × 164–177 μ wide), ornamented with small tubercles and punctations and bearing nine simple setae. Stigma situated between coxae III and IV ; peritremes not joined anteriorly (Text-fig. 170), and not extending posterior to the stigmata. Outer margin of peritreme crenate ; peritrematal shield extending to the posterior level of coxa IV. Metapodal shields narrow and transversely situated.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whiplike. All setae on pedipalp simple. Tectum (Text-fig. 171) three-pronged, typical of the genus. The dentition of the chelicera is shown in Text-fig. 172.

Leg I (360–366 μ long) with the tarsus (103–113 μ) longer than the tibia (58–63 μ). Setae on tarsus I very fine ; those on remaining segments stouter. Tarsi II–IV with a pair of lanceolate setae, and ambulacra with lateral lobes acuminate, median lobe rudimentary (Text-fig. 173). Tarsus I slightly swollen at its distal half, pulvillus and claws small.

MALE. Unknown.

LOCALITY. Argentina. The holotype female (1959.1.20.166) and three paratypes (1959.1.20.167–169) from horse dung and decomposing vegetable matter in forest, Quebrada de los Sosa, Tafí, Tucumán, 1,300 m., 17.v.1953, collected by Dr. P. Wygodzynsky.

Sejus tuberculatus sp. nov.

FEMALE. Dorsal shield (477–518 μ long × 310–330 μ wide) minutely punctured and slightly concave posteriorly (Text-fig. 174). " Anterior dorsal shield " with twenty-one pairs of simple setae. " Posterior dorsal shield " with fifteen pairs of simple setae ; J5 are the shortest. The distribution and relative lengths of the setae, and the ornamentation of the dorsal shield are shown in the Text-fig.

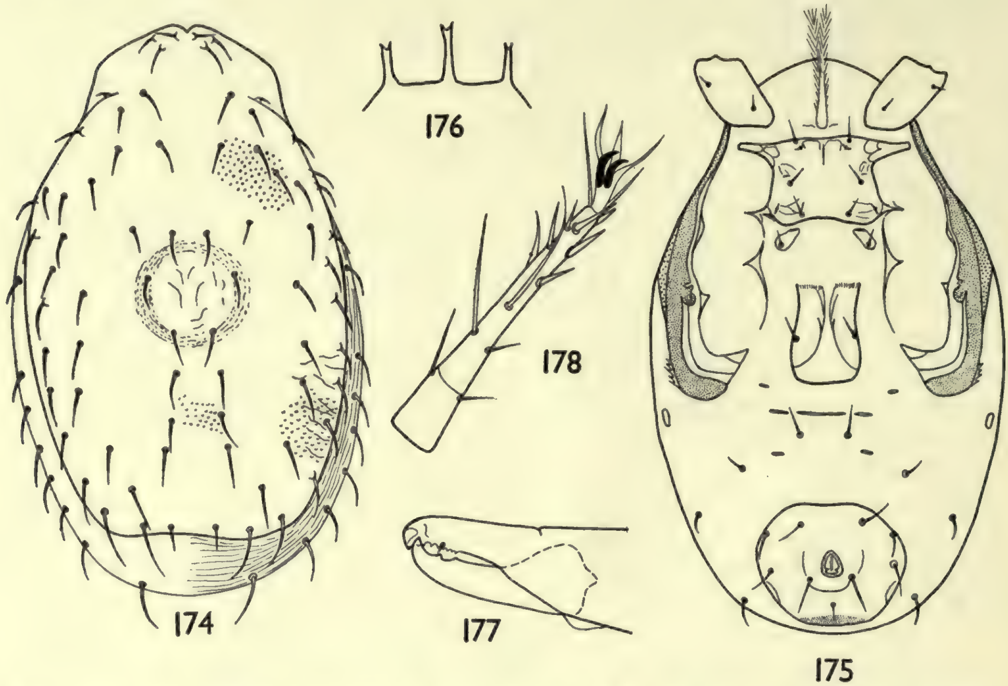
Tritosternum well developed and with pilose laciniae. Sternal shield with faint sculpturing, and bearing three pairs of simple setae (Text-fig. 175). Genital shield flask-shaped, and bearing a single pair of setae. Ventri-anal shield almost circular in outline (130–144 μ long × 144–147 μ wide) and bearing nine simple setae. Between the genital and ventri-anal shields lies a transverse row of about three narrow plates, and posterior to these lie two small plates. Stigma situated between coxae III and IV ; peritreme and peritrematal shields extending posterior to coxa IV. Metapodal plates small.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whiplike. All setae on pedipalp simple. Tectum (Text-fig. 176) three-pronged. The dentition of the chelicera is shown in Text-fig. 177.

Leg I (794–804 μ long) with the tarsus (162–177 μ) shorter than the tibia (182–

197 μ). Setae on tarsus, tibia and genu fine; those on other segments stouter; tarsal claws minute, inconspicuous. Tarsi II–IV with a pair of lanceolate setae; ambulacra with three acuminate lobes (Text-fig. 178).

MALE. Unknown.



FIGS. 174–178. *Sejus tuberculatus* sp. nov., female. Fig. 174, dorsum. Fig. 175, venter. Fig. 176, tectum. Fig. 177, chelicera. Fig. 178, tarsus II.

LOCALITY. Argentina. The holotype female (1959.1.20.170) and two paratype females (1959.1.20.171.172) from decaying vegetable matter in forest, Quebrada de los Sosa, Tafí, Tucumán, 13.v.1953, 1,300 m., collected by Dr. P. Wygodzynsky.

The following species also appear to belong to the genus *Sejus*, but with the exception of *Episeius groenlandicus*, have not been examined by us:

Acarus tendens Schrank, 1803. *Fauna Boica*, **3** : 209. Oudemans (1929) considers this species to be synonymous with *Platyseius subglaber* (Ouds.).

Gamasus scabriculus Nordmann, 1832. *Mikr. Beitr. Naturg. wirbell. Thiere* : 85.

Epicrius glaber Berlese, 1886. *A.M.S.*, 30, *No.* 9. Italy.

Hypoaspis scutulis Banks, 1914. *Psyche*, **21** : 161. Brazil.

Lasioseius borealis var. *temperatus* Berlese, 1916. *Redia*, **12** : 34. Palermo.

Lasioseius grandis Berlese, 1916. *Tom. cit.* : 34. Piemonte, Venice.

Lasioseius parapodicus Berlese, 1916. *Tom. cit.* : 35. Java.

Lasioseius similis Berlese, 1916. *Tom. cit.* : 35. Italy. This species may be a synonym of *Sejus serratus* (Halbert).

Lasioseius mutilus Berlese, 1916. *Tom. cit.* : 37. Florence.

Lasioseius (*Cheiroseius*) *alpestris* Berlese, 1916. *Tom. cit.* : 41. Italy.

Episeius major incisus Willmann, 1938. *Ann. Hist. nat. Mus. Hung.*, **31** : 168. Hungary.

Episeius groenlandicus Haarløv, 1942. *Medd. Grønland*, **128** : 18. Greenland.

Episeius aequalis Schweizer, 1949. *Rés. Rech. sci. Parc Nat. Suisse, N.F.* **2** : 64. Switzerland.

Episeius handschini Schweizer, 1949. *Tom. cit.* : 71. Switzerland.

Episeius salicorniae Willmann, 1949. *Veröff. Mus. Nat. Bremen, No. 1A* : 118. Poland.

Episeius longipes Willmann, 1951. *SB. öst. Akad. Wiss., Abt.* 1, **160** : 112. Austria.

Platyseius mackerassae Womersley, 1956. *J. Linn. Soc. Lond.* (*Zool.*) **42** : 552. Queensland.

Genus ***ZERCONOPSIS*** Hull

Zerconopsis Hull, J. E., 1918, *Trans. nat. Hist. Soc. Northumb.*, **5** : 65.

Platyseiine mites with the " posterior dorsal shield " bearing fourteen pairs of setae comprising five pairs in the J and the Z series but only four pairs in the S series (S2 being situated on the lateral interscutal membrane). Three to five pairs of dorsal setae stout and paddle-like (Text-figs. 179, 192). Lateral margins of the shield entire or incised anterior to S1. Sternal shield in the female with three pairs of setae ; metasternals situated on platelets. Genital shield wedge shaped, genital setae situated on or off the shield. Ventri-anal shield large and bearing from three to seven pairs of setae in addition to the three setae normally associated with the anus. Male with sterniti-genital and free ventri-anal shield. Peritreme without post-stigmatic process ; peritrematal shield poorly developed posterior to coxa IV. Chaetotaxy of the venter of the gnathosoma and of the pedipalps typical of the subfamily. Chelicerae chelate-dentate, movable digit in the male with a short spermatophoral process ; tectum basically three-pronged. Legs I–IV with a well-developed ambulacrum ; median lobes of pulvilli rounded apically.

Type species ***Gamasus remiger*** Kramer, 1876

Key to Species—Adults

1. Dorsal shield with distinct lateral incisions anterior to S1 (Text-figs. 184 and 197) 2
—Lateral margins of the dorsal shield entire 3

2. Genital shield in the female narrow, without setae (Text-fig. 198). Labrador
Z.l abradorensis sp. n. (p. 99)
—Genital shield in the female broad, with a pair of setae (Text-fig. 185). Switzerland
Z. muestairi (Schweizer) (p. 94)

3. Dorsal shield with five pairs of paddle-like setae (Text-fig. 192) ; genital shield without setae (Text-fig. 193). Hungary . . *Z. decemremiger* sp. n. (p. 96)

—Dorsal shield with three pairs of paddle-like setae (Text-figs. 179 and 189) ; genital shield with or without setae 4

4. Genital shield with a pair of setae (Text-fig. 180) ; with one pair of large, subtriangular metapodal shields. Europe . . . . . . *Z. remiger* (Kramer) (p. 92)

—Genital shield narrow, without setae (Text-fig. 190) ; with two pairs of metapodal shields. England . . . . *Z. michaeli* sp. n. (p. 95)

Zerconopsis remiger (Kramer)

Gamasus regimer Kramer, P., 1876, *Arch. Naturg.*, **42** : 93.
Ameroseius bispinosus Berlese, A., 1910, *Redia*, **6** : 253.

FEMALE. Dorsal shield (570–630 μ long × 310–382 μ wide) covered anterolaterally with a distinct reticulated pattern ; posterior and central areas with a lighter network (Text-fig. 179). " Anterior dorsal shield " with twenty-two pairs of setae of which one pair is paddle-like, the remainder simple ; verticals short, each on a tubercle. " Posterior dorsal shield " with fourteen pairs of setae of which two pairs are paddle-like and the remainder simple ; J5 are the shortest. The distribution and relative lengths of the dorsal setae and the ornamentation of the dorsal shield are shown in Text-fig. 179.

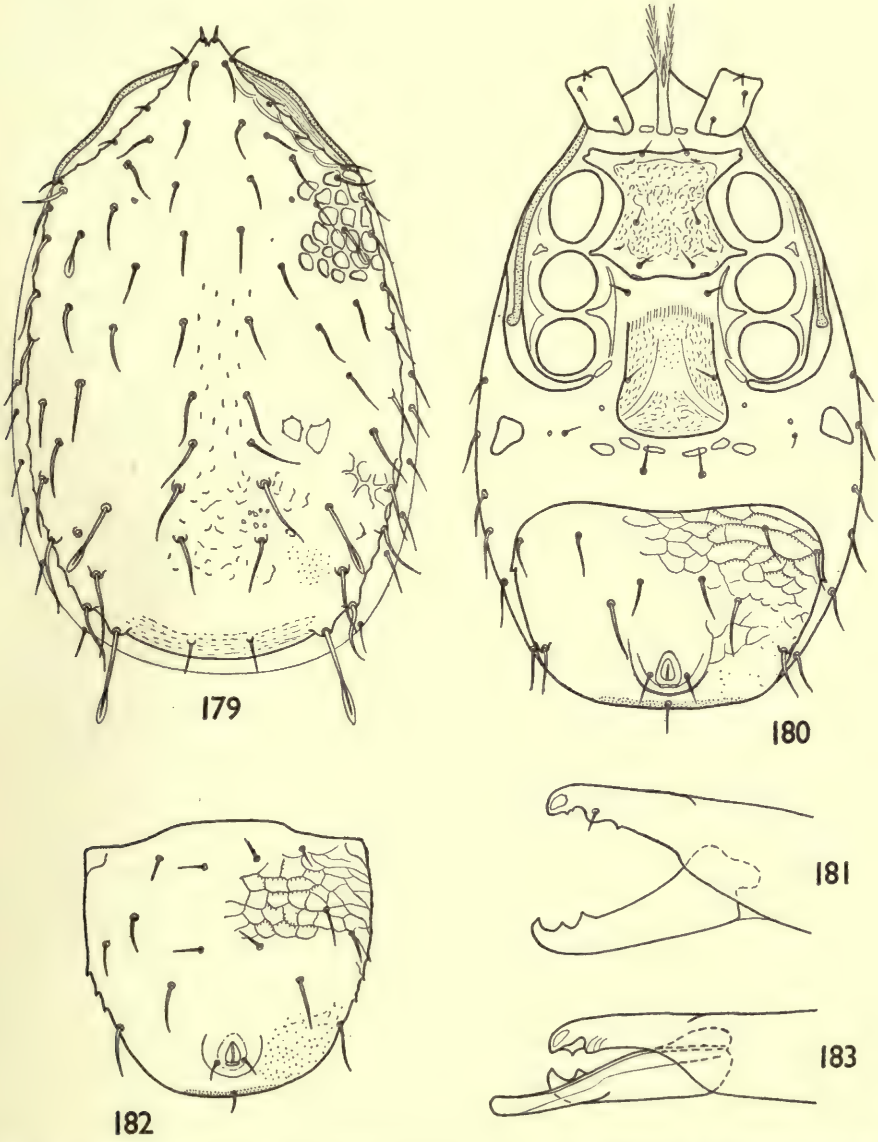
Tritosternum with a narrow base and pilose laciniae, and flanked by a narrow pair of pre-endopodal shields. Sternal shield with a fine granular pattern and bearing three pairs of simple setae (Text-fig. 180). Genital shield also with granular markings, and bearing one pair of setae. Ventri-anal shield wider than long (220–223 μ long × 225–303 μ wide), heavily reticulated and bearing thirteen simple setae. Between the genital and ventri-anal shields lie six platelets. Stigma situated between coxae III and IV with the peritreme not extending posterior to the stigma. Metapodal plates conspicuous.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum three-pronged and typical of the genus. The dentition of the chelicera is shown in Text-fig. 181.

Leg I (379–400 μ long) with the tarsus (99–103 μ) longer than the tibia (63–68 μ) ; claws small, pulvillus short. Tarsus I smooth with fine setae ; tibia, genu and femur with majority of setae arising from strong tubercles. Tarsi II–IV with a pair of lanceolate setae ; ambulacra with median lobes of pulvilli rounded apically.

MALE. Dorsal shield (530–550 μ long × 299–310 μ wide) with chaetotaxy and ornamentation similar to the female. Sterniti-genital shield with five pairs of simple setae. Ventri-anal shield (Text-fig. 182) reticulated anteriorly and bearing seventeen simple setae. The gnathosoma, tectum, pedipalps and legs are similar to those of the female. Leg I (c. 420 μ long) with the tarsus (99 μ) and the tibia (68 μ). Spermatophoral process about a third as long again as the movable digit of the chelicera (Text-fig. 183).

DISTRIBUTION. Kramer (1876) described this species from under fallen leaves without giving a locality, and Berlese (1910) described *Ameroseius bispinosus* from rotting leaves at Palermo. We have examined specimens from Nadap, Herkulesfürdo, and Gyertyánliget in Hungary, and British specimens from Goyt Valley, Cheshire, 24.xi.1940, collected by H. Britten; Rydal Water, Westmorland, 29.xi.1954, collected by M. E. Bacchus; Harefield, Middlesex, 22.i.1956, collected by A. H. G. Alston; and Avonmouth, Gloucestershire, 11.v.1957, collected by P. N. Lawrence.

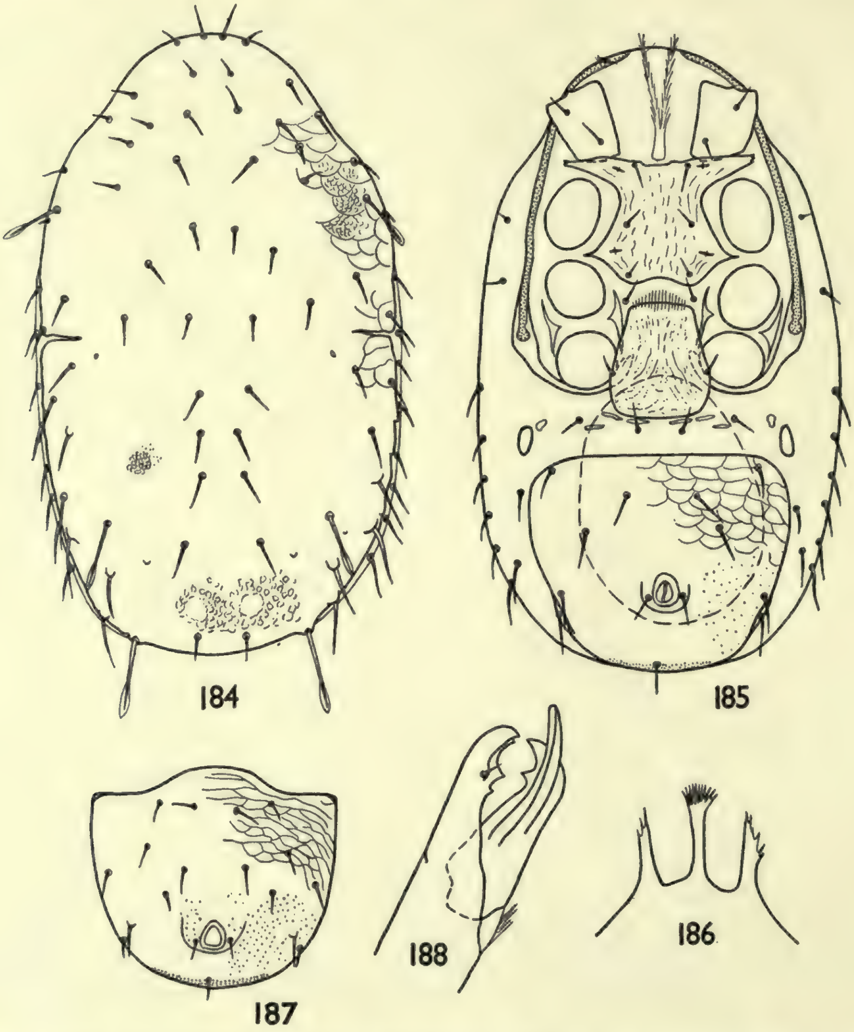


Figs. 179–183. *Zerconopsis remiger* (Kramer). Fig. 179, dorsum of female. Fig. 180, venter of female. Fig. 181, chelicera of female. Fig. 182, ventri-anal shield of male. Fig. 183, chelicera of male.

Zerconopsis muestairi (Schweizer) comb. nov.

Lasioseius müstairi Schweizer, J., 1949, *Réc. Rech. sci. Parc Nat. Suisse N.F.* **2** : 50.

FEMALE. Dorsal shield (585–630 μ long × 315–378 μ wide) with a lateral incision anterior to seta S1 ; lightly reticulated anteriorly and entirely granular (Text-fig. 184). " Anterior dorsal shield " with nineteen pairs of setae of which one pair is paddle-like, remainder simple ; verticals relatively long and well separated. " Posterior dorsal shield " with fourteen pairs of setae of which two pairs are paddle-like,



FIGS. 184–188. *Zerconopsis muestairi* (Schweizer). Fig. 184, dorsum of female. Fig. 185, venter of female. Fig. 186, tectum of female. Fig. 187, ventri-anal shield of male. Fig. 188, chelicera of male.

the remainder simple ; J5 are the shortest. The distribution and relative lengths of the dorsal setae and the form of the dorsal shield are shown in the Text-fig.

Tritosternum with a narrow base and pilose laciniae. Sternal shield with faint sculpturing and bearing three pairs of simple setae (Text-fig. 185). Genital shield also with faint markings, and bearing a single pair of setae. Ventri-anal shield wider than long (180–223 μ long × 240–270 μ wide), reticulated in its anterior half and bearing thirteen simple setae. Between the genital and ventri-anal shields lie six platelets. Stigma situated between coxae III and IV with the peritreme not extending posterior to the stigma. Metapodal plates small.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum (Text-fig. 186) three-pronged and typical of the genus. The chelicerae are figured by Schweizer (1949).

Leg I (432–504 μ long) with the tarsus (118–132 μ) longer than the tibia (68–75 μ). Claws on leg I distinct, pulvillus small ; tarsal setae fine, those on other segments stouter. Tarsi II–IV with a pair of lanceolate setae ; median lobes of pulvilli rounded apically.

MALE. Dorsal shield (467–498 μ long × 252–289 μ wide) with chaetotaxy and ornamentation similar to the female. Sterniti-genital shield with five pairs of simple setae. Ventri-anal shield with nineteen simple setae (Text-fig. 187). The gnathosoma, tectum, pedipalps and legs are typical. Leg I (326–332 μ long) with the tarsus 108–116 μ and the tibia 63–65 μ. The spermatophoral process and chelicera are shown in Text-fig. 188.

LOCALITY. This species is known only from the Swiss National Park. We have examined five females and three males from the type series.

Zerconopsis michaeli sp. nov.

FEMALE. Dorsal shield (498 μ long × 253 μ wide) with a heavy distinct pattern of depressions ; lateral margins irregular, posterior margin crenate (Text-fig. 189). " Anterior dorsal shield " with nineteen pairs of setae of which one pair is paddle-like, the remainder simple ; verticals on tubercles and directed anteriorly. " Posterior dorsal shield " with fourteen pairs of setae of which two pairs are paddle-like, the remainder simple. The distribution of the setae and the structure and ornamentation of the dorsal shield are shown in the Text-fig.

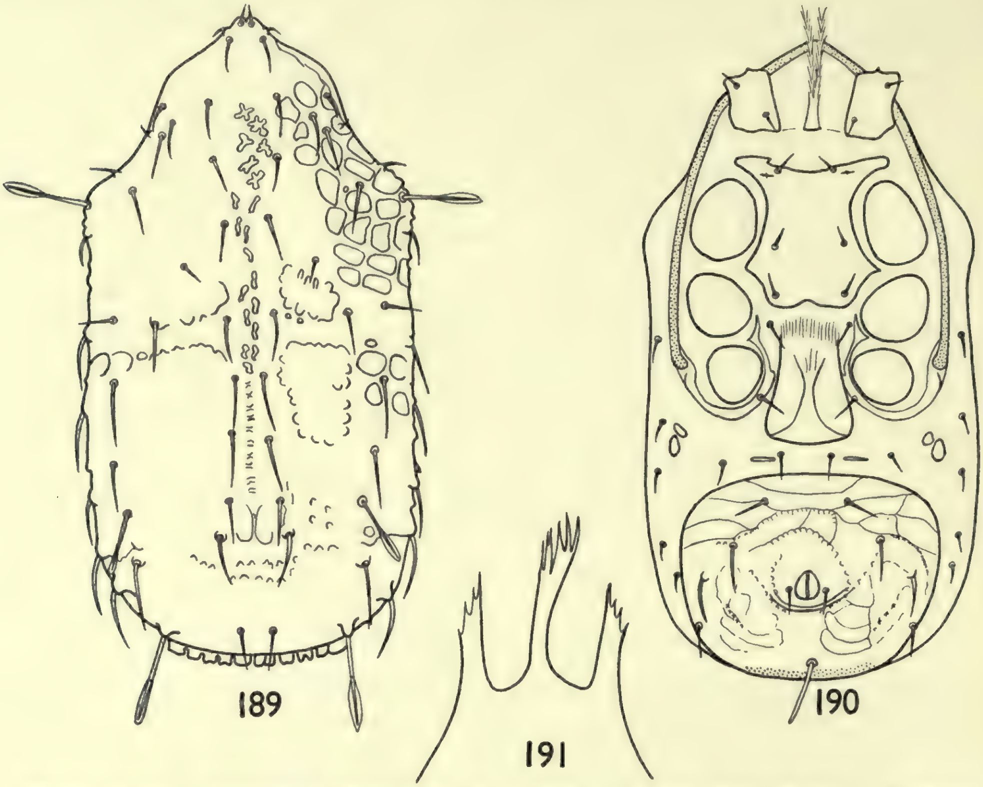
Tritosternum with a narrow base and pilose laciniae. Sternal shield plain, bearing three pairs of simple setae (Text-fig. 190). Genital shield narrow, setae off the shield. Ventri-anal shield wider than long (160 μ long × 212 μ wide), with a pattern of reticulations and dots, and bearing eleven setae of which the post-anal is long and stout. There are at least two narrow sclerotized platelets between the genital and ventri-anal shields. Stigma situated between coxae III and IV ; no post-stigmal prolongation of the peritreme. Metapodal plates small.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum (Text-fig. 191) three-pronged and typical of the genus. Chelicerae typical.

Leg I (387 μ long) with the tarsus (101 μ) almost twice the length of the tibia (58 μ). Legs II–IV incomplete in the unique specimen, but some of the setae arise from tubercles.

MALE. Unknown.

LOCALITY. A single female (1930.8.25.1840) from "England" in the A. D. Michael Collection and labelled "*Sejus remiger* Kramer".

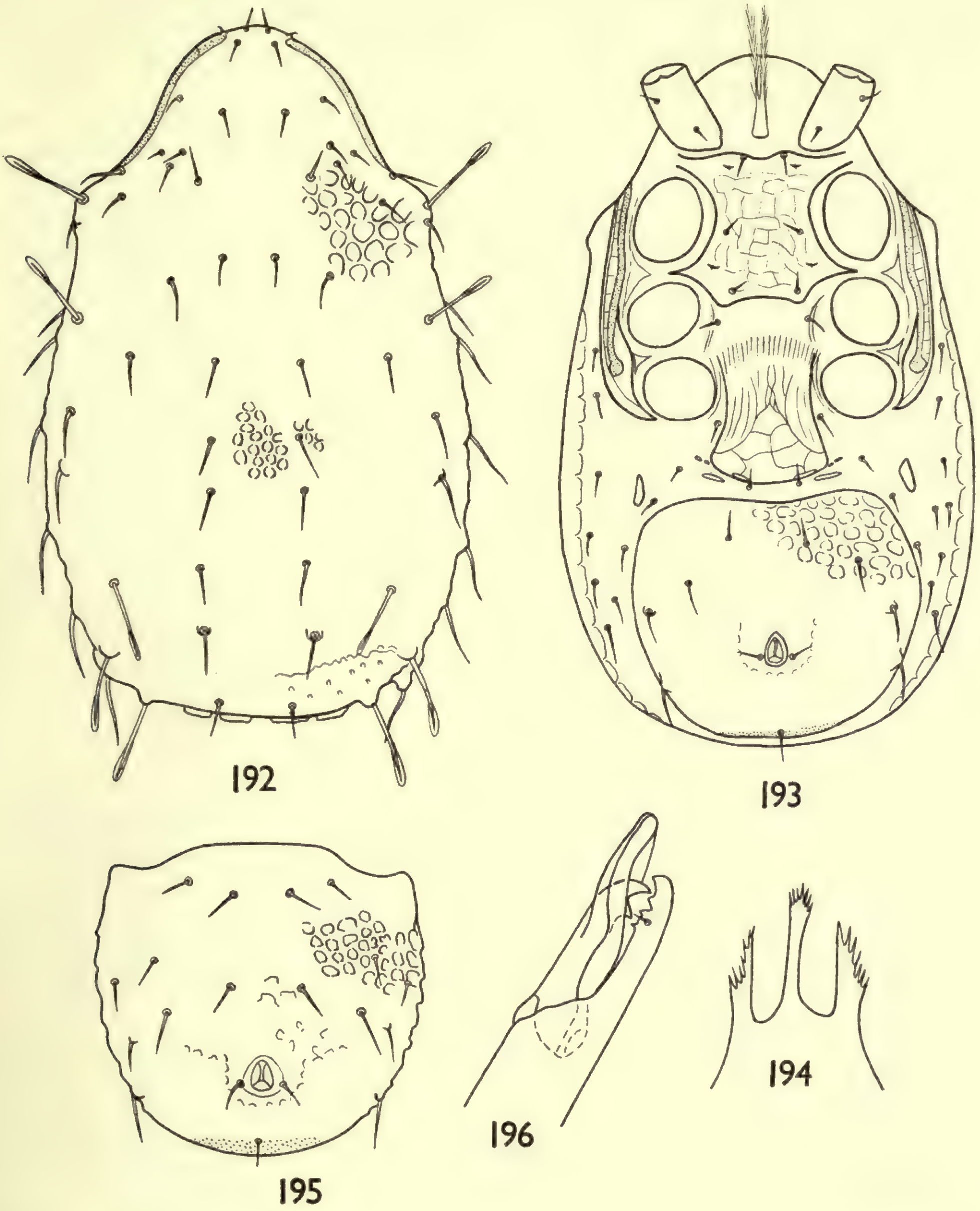


FIGS. 189–191. *Zerconopsis michaeli* sp. nov., female. Fig. 189, dorsal shield. Fig. 190, venter. Fig. 191, tectum.

Zerconopsis decemremiger sp. nov.

FEMALE. Dorsal shield (590–600 μ long × 360–382 μ wide) with a dense pattern of depressions, largest around the anterior margin and becoming smaller posteriorly (Text-fig. 192). "Anterior dorsal shield" with twenty pairs of setae of which two pairs are paddle-like, the remainder simple ; verticals separated by about three times the diameter of their bases. "Posterior dorsal shield" with fourteen pairs of setae of which three pairs are paddle-like ; J5 are the shortest. The distribution of the setae and the ornamentation of the dorsal shield are shown in the Text-fig.

Tritosternum with a narrow base and pilose laciniae. Sternal shield with faint



FIGS. 192–196. *Zerconopsis decemremiger* sp. nov. Fig. 192, dorsal shield of female. Fig. 193, venter of female. Fig. 194, tectum of female. Fig. 195, ventri-anal shield of male. Fig. 196, chelicera of male.

reticulations and bearing three pairs of simple setae (Text-fig. 193). Genital shield reticulated; genital setae off the shield. Ventri-anal shield wider than long (205–220 μ long × 253–263 μ wide), with a conspicuous pattern of small depressions and bearing eleven simple setae. Between the genital and ventri-anal shields lie four small plates. Stigma situated between coxae III and IV; peritreme without post-stigmal prolongation. Metapodal plates small.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum three-pronged and typical of *Zerconopsis* (Text-fig. 194): chelicerae also typical.

Leg I (434 μ long) with the tarsus (111–116 μ) longer than the tibia (68–70 μ). Claws on leg I small; tarsal setae fine, those on remaining segments somewhat stouter and arising mainly from small tubercles. Tarsi II–IV with a pair of lanceolate setae. Ambulacra with median lobes of pulvilli rounded apically.

MALE. With dorsal shield (507–550 μ long × 289–330 μ wide) essentially the same as the female. Sterniti-genital shield with five pairs of simple setae. Ventri-anal shield (Text-fig. 195) similar in ornamentation to the female and bearing nineteen simple setae. The gnathosoma, tectum, pedipalps and legs are similar to those of the female. Leg I (434 μ long) with the tarsus (111–113 μ) longer than the tibia (68–70 μ). The spermatophoral process and chelicera are shown in Text-fig. 196.

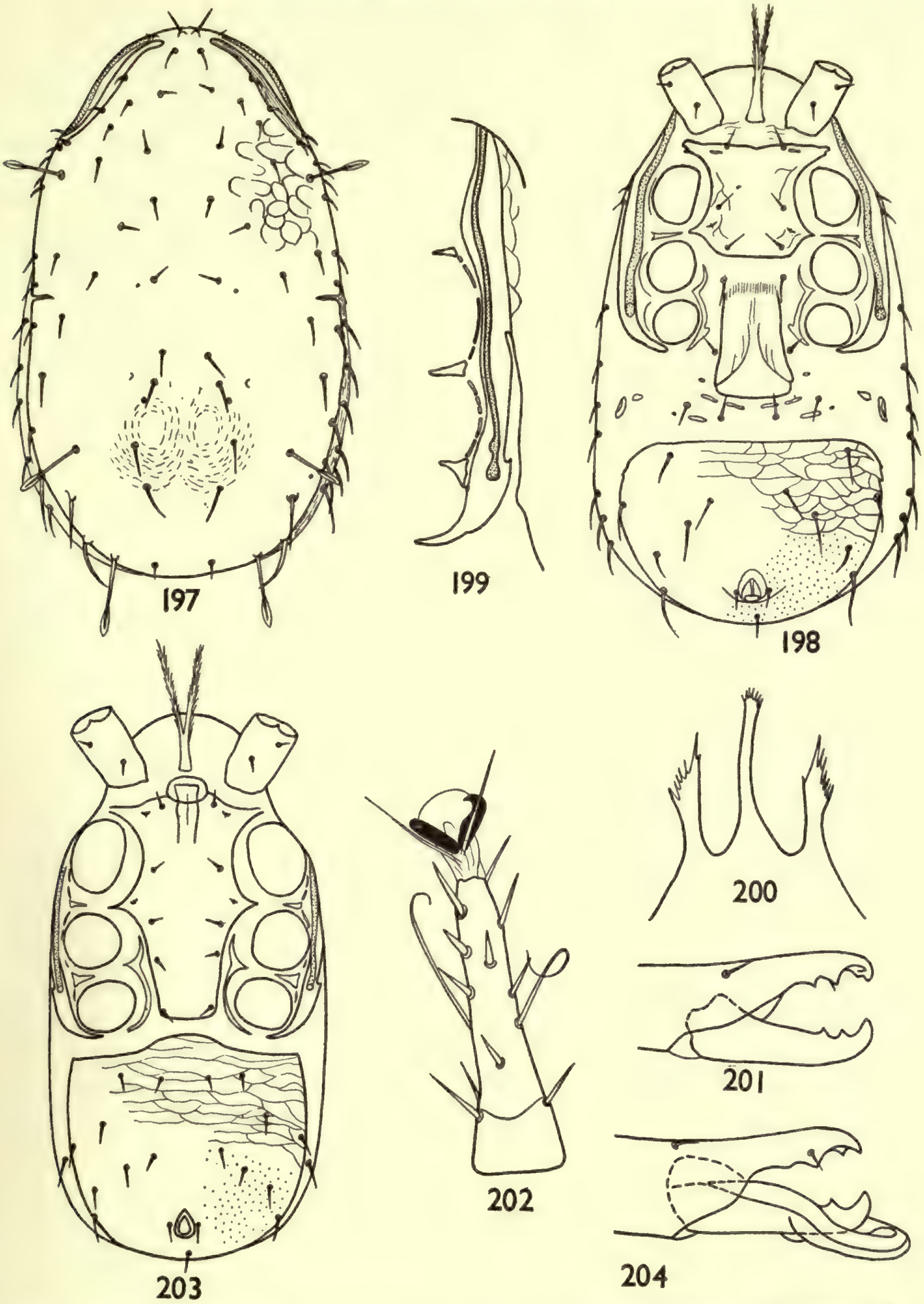
LOCALITY. Hungary. The holotype female (1959.1.20.177), allotype male (1959.1.20.178), four female and two male paratypes (1959.1.20.179–184) from Herkulesfürdo, April–June, 1938; and four female and two male paratypes from Gyertyánliget, 6–17th August, 1940, sent to us by Dr. J. Balogh, Budapest.

Zerconopsis labradorensis sp. nov.

FEMALE. Dorsal shield (581–609 μ long × 299–320 μ wide) with a lateral incision anterior to seta S1, reticulated antero-laterally and the remainder granulate (Text-fig. 197). "Anterior dorsal shield" with twenty-one pairs of setae of which one pair is paddle-like, the remainder simple; vertical setae with their bases two diameters apart. "Posterior dorsal shield" with fourteen pairs of setae of which two pairs are paddle-like; J5 are the shortest. The distribution of the setae and the form of the dorsal shield are shown in the Text-fig.

Tritosternum with a narrow base and a pair of pilose laciniae. Sternal shield almost without markings, and bearing three pairs of simple setae (Text-fig. 198). Genital shield plain; setae off the shield. Ventri-anal shield wider than long (177–215 μ long × 253–260 μ wide), reticulated anteriorly and granulate posteriorly, and bearing fifteen simple setae. Between the genital and ventri-anal shields lie six small sclerotized plates. Stigma between coxae III and IV; peritreme without post-stigmal prolongation (Text-fig. 199). Metapodal plates small.

Venter of gnathosoma with rostral and internal palptrochanter setae long, whip-like. All setae on pedipalp simple. Tectum (Text-fig. 200) three-pronged; chelicerae typical (Text-fig. 201).



FIGS. 197–204. *Zerconopsis labradorensis* sp. nov. Fig. 197, dorsum of female. Fig. 198, venter of female. Fig. 199, peritrematal shield of female. Fig. 200, tectum of female. Fig. 201, chelicera of female. Fig. 202, tarsus II of female. Fig. 203, venter of male. Fig. 204, chelicera of male.

Leg I (462–502 μ long) with the tarsus (124–134 μ) twice the length of the tibia (65–73 μ); tarsal claws small; setae fine, those on remaining segments shorter and stouter. Tarsi II–IV (Text-fig. 202) with a pair of lanceolate setae; ambulacra with median lobes of pulvilli rounded apically.

MALE. Dorsal shield (488 μ long × 238 μ wide) essentially the same as in the female. Sterniti-genital shield with five pairs of simple setae. Ventri-anal shield (Text-fig 203) similar in ornamentation to the female and bearing nineteen simple setae. The gnathosoma, tectum, pedipalps and legs are similar to those of the female. Leg I (462 μ long) with the tarsus (124 μ) twice as long as the tibia (65 μ). The spermatophoral process of the chelicera is shown in Text-fig. 204.

LOCALITY. Labrador. The holotype female (1959.1.20.185), allotype male (1959.1.20.186) and six paratype females (1959.1.20.187–192) from wet willow humus, West Carter Basin, 4–17.viii.1958, collected by P. N. Lawrence during the British Schools' Exploring Society Expedition.

SUMMARY

1. This paper deals with the external morphology and classification of the Platyseiinae. Four genera, namely, *Sejus* C. L. Koch (syn. *Cheiroseius*, *Episeius* and *Episeiella*), *Platyseius* Berlese, *Zerconopsis* Hull, and *Plesiosejus* gen. nov. are recognized. Keys are given to the species represented in the Collections of the British Museum (Natural History).

2. The following new synonymy is introduced:

Lasioseius (*Platyseius*) *capillatus* Berl. = *Hypoaspis subglabra* Oudms.
Paraseius tenuipes Halbert = *Ameroseius italicus* Berl.
Episeiella heteropoda Willm. = *Sejus viduus* C. L. Koch
Episeius montanus Willm. = *Ameroseius borealis* Berl.
Episeius ovaspini Schweizer = *Lasioseius* (*Episeius*) *glaber* var. *curtipes* Halbt.
Parasejus glaber var. *minor* Trägårdh = *Epicrius laelaptoides* Berl.
Lasioseius (*Episeius*) *sphagni* Halbt. = *Epicrius laelaptoides* Berl.

3. The following twenty-seven new species are described and figured: *Platyseius jamaicensis*; *Platyseius spinosus*; *Plesiosejus horridus*; *Sejus aciculatus*; *S. alstoni*; *S. antillanus*; *S. areolatus*; *S. bellingeri*; *S. browningi*; *S. cassiteridum*; *S. clayi*; *S. dromadis*; *S. hulli*; *S. jamaicensis*; *S. kennedyi*; *S. neborealis*; *S. nepalensis*; *S. nodosus*; *S. ornatus*; *S. parbatensis*; *S. phalangioides*; *S. signatus*; *S. spinipes*; *S. tuberculatus*; *Zerconopsis decemremiger*; *Z. labradorensis* and *Z. michaeli*.

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BRITISH SLUGS
(PULMONATA; TESTACELLIDAE, ARIONIDAE, LIMACIDAE)

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BY

H. E. QUICK

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NATURAL HISTORY

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BRITISH SLUGS (PULMONATA; TESTACELLIDAE, ARIONIDAE, LIMACIDAE)

By H. E. QUICK

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INTRODUCTION

No comprehensive work on British slugs has appeared since John William Taylor's classic monograph (1902–07). Besides full information on their nomenclature, systematics and biology, this contains excellent coloured plates, depicting numerous varieties of the eighteen species of slugs which he recognized as British. Besides much information on these species which has become available since 1907, five more species, a subspecies, and two aliens established in British greenhouses must be added to the list. Taylor omitted *Arion lusitanicus* (p. 135), although it had already been recorded from Britain, and it has since reappeared. *Milax budapestensis* (p. 160), another species of *Milax* provisionally referred to *M. insularis* (p. 156) and *Agriolimax caruanae* (p. 175) have been recorded ; *Agriolimax reticulatus* (p. 164) has been shown to be specifically distinct from *A. agrestis,* and *Arion ater rufus* (p. 145) to be subspecifically distinct from *A. ater.* The alien species *Lehmannia poirieri* (p. 197) and *Limax nyctelius* (p. 202) have been found in Britain, but only in greenhouses. Two names used by Taylor must be changed : *Arion circumscriptus* to *A. fasciatus* (p. 127) and *Limax arborum* to *Lehmannia marginata* (p. 194).

Two more recent works also deal with all British slugs, though less completely. Ellis (1926) gives monochrome figures but only occasional references to internal anatomy ; while Quick (1949) also gives monochrome figures, and information relating mainly to identification in the field. Among more general works, Kunkel (1916) on the biology of pulmonates, Økland (1923) on the Arionidae of Norway, and Boycott (1934) on the habits of British land molluscs may be especially mentioned. Much information on courtship and copulation is given by Gerhardt (1933, 1935, 1939 and 1940), on the seasonal abundance and growth of slugs in gardens and fields by Barnes & Weill (1945, with good coloured plates of garden species), and on their ecology by Thomas (1944). For full synonymies, reference should be made to Kennard & Woodward (1926), and also to Taylor (1902–07) and Hesse (1926). Only the more important synonyms are quoted below.

The group of naked pulmonates termed slugs is highly polyphyletic in origin. British slugs belong to the three families Testacellidae, Arionidae and Limacidae, which have evidently been derived from shelled Oleacinids, Endodontids and Zonitids respectively.

Arrangement

Information is given in the same sequence for each species (except that the shell is described before the external variations for *Testacella*) under the following headings, any of which may be omitted.

Notes
First British record
Diagnostic features
External appearance
External variation
Shell
Pallial organs
Pedal gland
Retractor muscles
Nervous system
Jaw
Radula
Alimentary system
Reproductive system
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Mating
Development
Behaviour
Ecology
Distribution
Fossil record
Material examined

The anatomical terms used in the descriptions are explained by means of a glossary and semi-diagrammatic figures on p. 203. Distributions in the British Isles are shown on vice-comital maps (p. 205), as well as being briefly described under " distribution ".

Acknowledgments

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NATIVE AND NATURALIZED SPECIES

Order STYLOMMATOPHORA

Pulmonate mollusca bearing eyes at the apex of retractile tentacles.

Superfamily OLEACINACEA

Jaw rudimentary or absent, radular teeth aculeate, shell turreted or auriform. Carnivorous.

Family TESTACELLIDAE

Shell small, auriform, situated at the posterior end of the body, covering the pallial organs. The upper tentacles (ommatophores) are not bulbous at the apex. There is no caudal mucus gland. A pair of lateral grooves with side branches directed obliquely upwards and forwards, and downwards and forwards, arises from a peripallial groove. The pedal mucus gland lies free in the body cavity. The cerebral commissure is very short, and the cerebro-pleural and cerebro-pedal commissures long. There is no jaw. The buccal bulb is enormous. The long narrow radular teeth, barbed at the apex, are disposed in transverse V-shaped rows, and a central tooth may be absent. The stomach is feebly developed and the anus lies just within the pulmonary cavity posteriorly. The kidney is without a secondary ureter. An osphradium is said to be present in a groove in the floor of the mantle cavity (Plate, 1891). The vagina is without accessory glands, and the right ocular retractor muscle passes forwards between the penis and vagina. *Testacella* is carnivorous, feeding on earth-worms and occasionally on other slugs, and is largely subterranean in habit.

Genus ***TESTACELLA*** Draparnaud, 1801

Type species *Testacella haliotidea* Draparnaud, 1801.

The sole genus, with the characters of the family. Through adaptation to a life spent largely underground, and a diet of earth-worms, the structure of *Testacella* has been profoundly modified. The relatively large shell and mantle cavity of other snails have been greatly reduced in size, and the body anterior to these structures elongated to accommodate the enormous buccal bulb with its powerful muscles and barbed radular teeth. The backwards shift of the pallial region is accompanied by a clockwise rotation of 180°, so that the heart and pericardium lie on the right side of the kidney with the ventricle in front of the auricle. The normal backwardly-directed loop of the intestine is obliterated, and the rectum runs backwards instead of forwards to the anus (beside the pulmonary orifice, at the rear).

It is convenient to gather together the available information on the life history of all the three British species of *Testacella*. A recent paper by Stokes (1958) gives further information, supplementing that of Barnes & Stokes (1951).

Mating

Little is known, but Gerhart (1940 : 579) reports that while unpacking a container he found a pair of *T. scutulum* in coitus in the moss, and accidentally separated them.

The penes were bluish-white, translucent, elongated, dorso-ventrally flattened cones, withdrawn from the adjacent vaginal openings. No appendix was visible, and the penes were of the simplest type occurring in land pulmonates. They quickly disappeared within the owners' bodies, and no more was to be seen. Barnes & Stokes (1951) found that the coitus of *T. haliotidea* and *T. scutulum* took place under the surface of the soil in their containers, the animals lying head to head: they do not mention any visible everted organs. Chemin (1939*a* and *b*) reports self-fertilization in *T. haliotidea* isolated when young.

Development

The eggs are ellipsoidal, with a white calcareous shell which becomes yellow, and are laid underground. Those of the three British species are distinguished only by differences in size: 5 × 4 mm for *T. maugei*, 7 × 4 mm for *T. haliotidea*, and 4 × 3 mm for *T. scutulum*. Barnes & Stokes confirm the old statement that they explode when placed on a warm hand. The eggs of *T. maugei* are laid in groups of 8–15 during the summer months, those of *T. haliotidea* and *T. scutulum* in captivity (Barnes & Stokes, 1951) in batches of 2–14 in March, 54–95 days after mating. Taylor (1902–07) records the time of development as 30–35 days for *T. maugei*, 20–36 days for *T. scutulum* and (quoting Gassies, 1849) 10–22 days for *T. haliotidea*. However, Barnes & Stokes found that embryonic development takes much longer than this for the latter two species: 144–201 days, or five to six months.

Like all our slugs and some, perhaps all, of the shell-bearing Stylommatophora except *Succinea* (which lacks a caudal vesicle), *Testacella* exhibits in the middle and late stages of development a haemocoelic cephalic vesicle protruding beneath the mantle over the head, containing part of the viscera; and a caudal haemocoelic vesicle projecting beyond the tail, which contains only haemocoelic fluid and corpuscles. The caudal vesicle varies in shape from genus to genus (see Text-fig. 18). In *Testacella* it is a flattened bilobed or broadly cordate sac (Text-figs. 1 D and 18 C). The two vesicles pulsate, expanding and contracting alternately so that haemocoelic fluid is driven back and forth, at a rate depending on the temperature. The vesicles may have an excretory or a respiratory function. The cephalic vesicle is withdrawn with its contents into the body, and shortly before hatching the caudal vesicle also shrinks and disappears. In *Testacella*, with its posterior mantle, the cephalic vesicle does not extend over the head (at any rate in the later embryonic stages).

Behaviour

It has been noted (Adams, 1941) that dust sprinkled on *Testacella* leads to copious discharge of fluid which washes it away. Another phenomenon does not seem to have been recorded. When lightly irritated, *Testacella maugei* partially contracts, and sometimes a forcible discharge of air and froth occurs in the middle line from under the front of the mantle edge, with a distinct high-pitched hissing sound. Presumably a communication to the lung cavity exists, and air is expelled by closure of the pulmonary orifice and muscular contraction. No duct is apparent on gross dissection, but serial section of the area show spongy tissue leading to the anterior expansions of the pulmonary cavity, through which air might be expelled. In its underground travels, or if dragged into a burrow by an attacked earth-worm, it is easy to imagine that earth could become impacted under the mantle border, and that the forcible expulsion of air and fluid would serve to dislodge it.

Ecology

Mostly to be found in gardens, allotments and other cultivated ground. During the day *Testacella* remains underground, retreating deeper in dry weather but sometimes hiding under stones and herbage in damp weather ; while at night it crawls freely on the surface. In the winter it hibernates in a strongly contracted state, in an underground cell. On slowly approaching a worm, the slug shoots out its radula and impales its prey at one end or in the middle, and engulfs it within a few minutes. Another worm may be eaten after a day or two. The faeces are very small in bulk and contain discarded radular teeth, fragments of worm cuticle and setae, and sometimes small white bodies which may be from the calcareous oesophageal glands of worms. *Testacella* is also said to eat other slugs.

Testacella maugei Férussac, 1819

Testacella maugei Férussac, 1819 : 94, pl. 8, figs. 10 and 12. Teneriffe.
Testacella aurigaster Watson, 1915 : 221 (from Layard MS.).

Notes

The type was found in 1796 by M. Maugé ; who died before publishing an account. According to Turton (1831 : 27), it was sent in 1812 from Dr. Leach at Bristol to Férussac. *T. aurigaster* refers to this species, introduced into South Africa (Watson, 1915 : 221).

First British record

By Férussac (1819).

Diagnostic features

Pear-shaped appearance (body widest behind) ; shell large (14 × 7 mm) ; two median lines of dorsal tubercles conspicuous, especially in the young ; lateral grooves wide (5 mm) apart at origin. Buccal bulb lacks lateral retractors ; cephalic retractors arise asymmetrically, from left side. Penis swollen posteriorly, lacks the flagellum of *T. haliotidea* ; penial retractor arises from body-wall about two-thirds of the way back ; vas deferens convoluted near free oviduct ; spermatheca duct long and slender, swollen proximally.

External appearance (Pl. 1, fig. 13)

Length when extended, 6–10 cm. The most bulky part of the body lies behind the centre. The lateral grooves are separated by about 5 mm at their origin from the peri-pallial groove, and each gives rise to about fourteen dorsal and ventral grooves directed obliquely forwards, which subdivide to produce the reticulate surface pattern. The row of tubercles on each side of the median dorsal line is more prominent than the other dorsal rows, especially in the young. The upper tentacles, bearing the small black eyes, are not bulbous at the apex, and the lower tentacles are short. The true pedal groove is only distinct for a few millimetres at the front of the foot fringe, but a peripodial groove above this runs to the tail. There is no caudal mucus gland. When crawling on a glass plate, the yellow sole is seen to be obscurely tripartite. The mucus is clear and viscid, drawing out into thin threads. The body is usually some shade of brown more or less sprinkled with darker spots, paler on the sides, and the sole is yellow or pink. The mantle is speckled with black, and the paler margin slightly overlaps the shell. The posterior respiratory orifice is bounded by the right and left mantle lobes.

Shell (Text-fig. 1 A)

The shell measures about 14 × 7 mm, and has a brown periostracum, often abraded. It is more convex than the shells of the other two species, and the columella does not show the same callous enlargement at the hinder end. The crescentic muscle scar is visible on the under surface.

External variation

Variety *aperta* Taylor (1902) has the shell wider and flatter than normal. Varieties *albina, griseonigrescens, viridans* and *griseorubescens* Gassies & Fischer (1856), *nigra* Collinge (1898) and *aurea* Taylor (1902) are colour varieties, whose characteristics are suggested by their names.

Pallial organs (Text-figs. 2 D and F)

The respiratory cavity, bounded by the right and left mantle lobes, leads to the pulmonary chamber, which is bounded by spongy vascular tissue. Anterior to this, the chamber is prolonged forwards as thin-walled air sacs projecting into the visceral cavity. The somewhat quadrate kidney, opening without a secondary ureter at the back of the chamber, lies above and in front of the pulmonary chamber. The pericardium lies to the right of the kidney and the ventricle is anterior to the auricle, and both branches of the aorta run forwards. The rectum runs obliquely in the pulmonary chamber to terminate in the anus just above and on the left of the respiratory orifice. The kidney projects over the apex of the left liver lobe. An osphradium is represented by a ridge of cells in the floor of the respiratory chamber, and is innervated from the right visceral ganglion (Plate, 1891).

Retractor muscles (Text-fig. 1 E)

Both the cephalic retractor muscles arise from the body-wall on the left side. The right ocular retractor passes between the penis and the vagina, and a branch takes the same course to the side of the head. The slender penial retractor arises from the right body wall about two-thirds of the way back, and not from the posterior end as it does in *T. haliotidea* and *T. scutulum.*

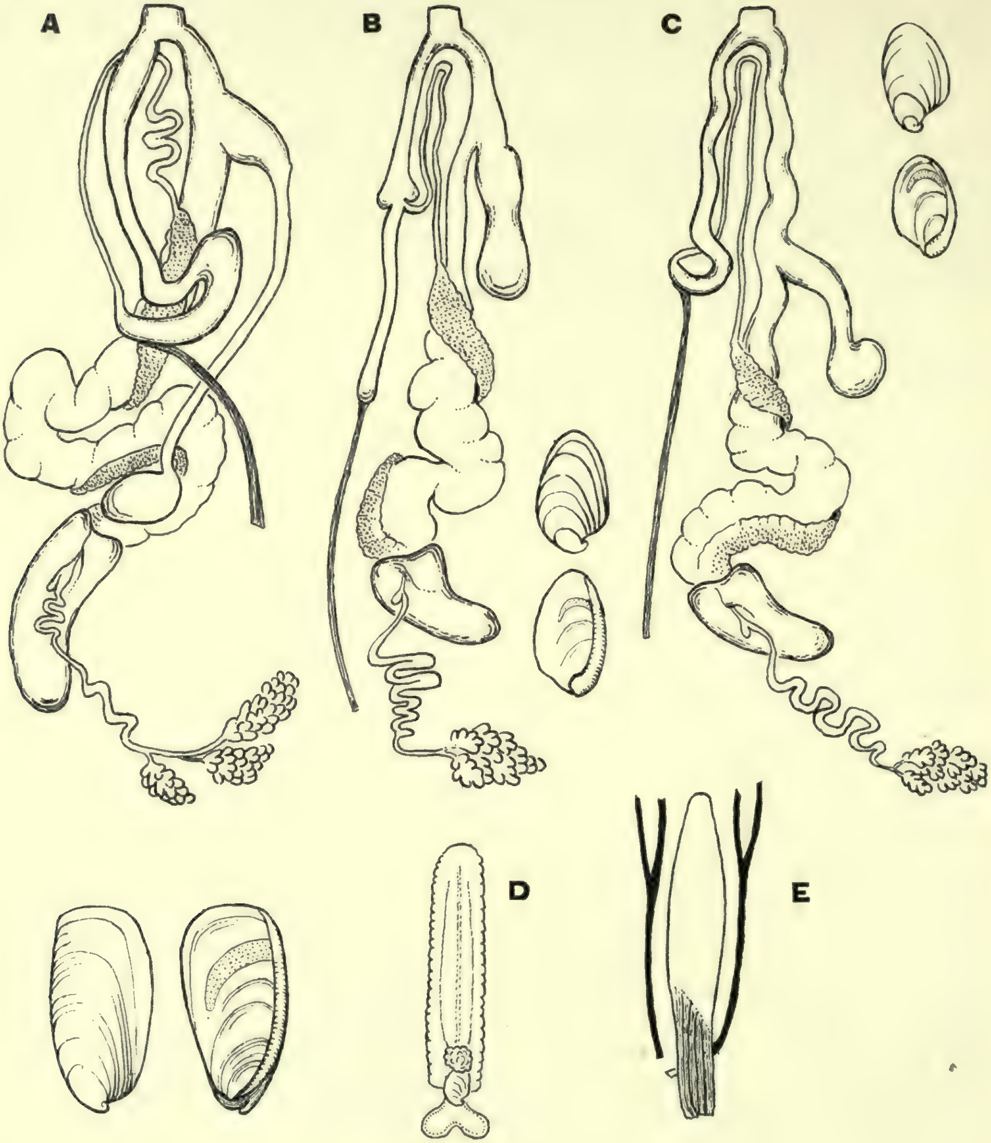

FIG. 1. *Testacella*. Reproductive organs (× 3·3), shell (× 2). **A.** *T. maugei*—shell below. **B.** *T. haliotidea*—shell right, below. **C.** *T. scutulum*—shell right, above.

D. *T. scutulum*—advanced embryo (× 6·7) showing cephalic vesicle in front of shell and caudal vesicle posteriorly. **E.** *T. maugei*—buccal bulb and ocular retractors.

Nervous system (Text-fig. 2 E)

The cerebral commissure is very short, and the cerebro-pleural and cerebro-pedal commissures are long to embrace the large buccal bulb. The buccal ganglia are large. The five visceral ganglia are close together, but not fused.

Radula (Text-fig. 2 A)

In each row, sixteen aculeate barbed teeth on each side of a small median tooth increase in size up to the penultimate one, while the sixteenth is much smaller. There are about fifty V-shaped rows.

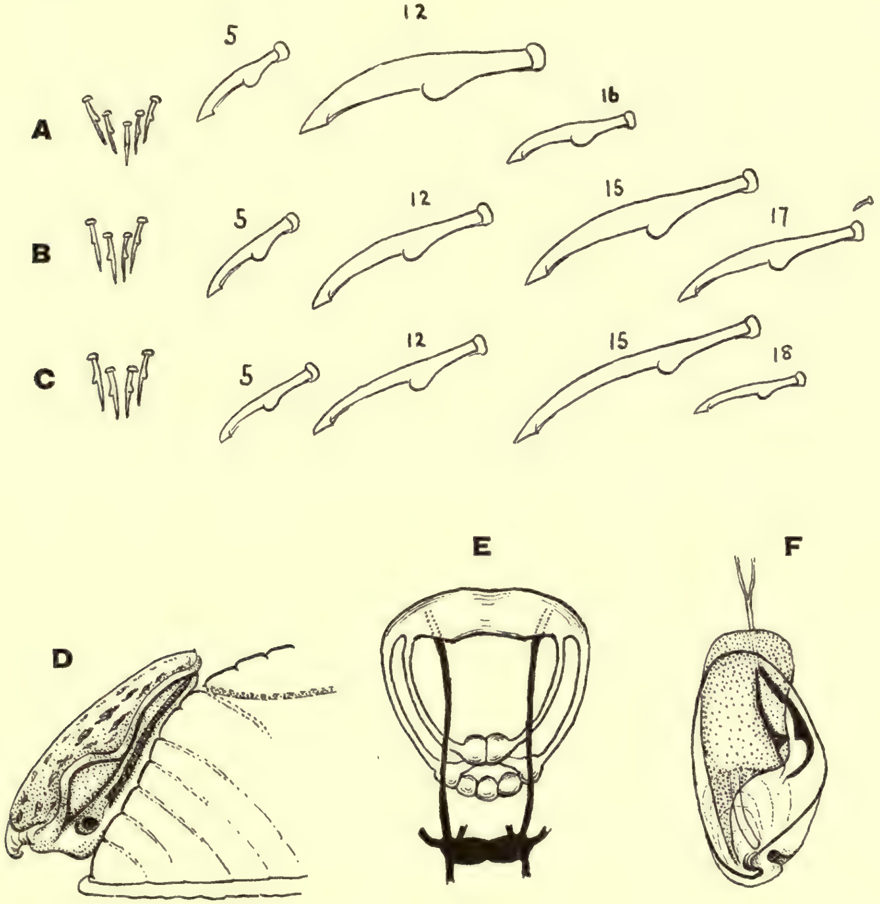

Fig. 2. *Testacella.* Representative radular teeth (× 67). **A.** *T. maugei*—showing central tooth. **B.** *T. haliotidea*—showing absence of central tooth. **C.** *T. scutulum*—showing absence of central tooth.

T. maugei. **D.** Posterior end of body (× 3·3) with shell removed and right mantle lobe reflected to expose respiratory orifice. **E.** Central nervous system, showing buccal ganglia (black) posterior to cerebral ganglia when animal is contracted. **F.** Pallial region, viewed as if shell were transparent.

Alimentary system

The buccal bulb, which is large but does not extend as far back as in *T. haliotidea* and *T. scutulum*, lacks lateral muscles but has a bundle of from two to four pairs of powerful muscles at the posterior end, attached to the diaphragm towards the left of the mid-line (Text-fig. 1 E). The small stomach is scarcely wider than the oesophagus and intestine. It receives the right and left liver ducts, and the left liver lobe forms the apex of the visceral mass. The intestine makes one forwardly-directed loop, and the long rectum runs backwards to the anus, close to the respiratory orifice.

Reproductive system (Text-fig. 1 A)

The reproductive organs are simple. The pale ovotestis lies at the apex of the visceral mass between the right and left lobes of the liver. The slightly sinuous hermaphrodite duct becomes slender and folded before entering the long narrow albumen gland, and bears a small seminal vesicle. The convoluted vas deferens, arising from the yellow ribbon-like prostate, runs forwards beside the free oviduct and then turns backwards, beneath the right ocular retractor to the apex of the penis. The penis is about 9 mm long, slender in front and dilated posteriorly and often folded over forwards. The mucous membrane is papillate at the apex and longitudinally ridged beyond, and there is no penial papilla. There is no caecum or flagellum. The penial retractor, arising from the right body wall about two-thirds of the way back, is inserted at the apex of the penis. The atrium is short and opens below the right upper tentacle. The free oviduct and vagina are wider than the penis. The long slender spermatheca duct is dilated at its origin from the oviduct, and enters the spermatheca sac laterally. The mucous membrane of the duct is longitudinally ridged, the ridges being more prominent in the bulbous part of the duct.

Mating, Development, Behaviour, Ecology

See pp. 108–110. The eggs measure 5 × 4 mm.

Distribution (Map 1)

T. maugei is the most westerly of the three British species of *Testacella*, known from Tangier, south-western Spain, Portugal, Brittany, Dieppe and the Atlantic isles (and introduced into North America and South Africa). In England and Wales it occurs west of a line from Cheshire to Middlesex, and in Ireland south-east of a line from Dublin to Cork. It is probably truly native only in the south-west.

Fossil record

Holocene and Recent.

Material examined

Living specimens from Singleton Park Botanical Gardens, Swansea, Glamorgan. Spirit material from various British localities, the Azores and Madeira.

Testacella haliotidea Draparnaud, 1801

Testacella haliotidea Draparnaud, 1801 : 99. ? Montpellier.
Testacella europea de Roissy, 1805, **5** : 252.

First British record

By Lukis (1834), from Guernsey.

Diagnostic features

Less bulky posteriorly, when extended, than *T. maugei* ; shell much smaller, (7 × 5 mm), columella somewhat truncate anteriorly, with conspicuous callous enlargement posteriorly ; dorsal tubercles not especially prominent ; lateral grooves close together at origin. Buccal bulb with powerful lateral retractors ; cephalic retractors arise symmetrically. Radula lacks a central tooth, apophyses of marginal teeth nearly central. Penis with flagellum and short apical caecum ; penial retractor arises from diaphragm at posterior end of body ; spermatheca duct short and bulbous.

External appearance (Pl. 1, fig. 10)

Length when extended, 8–12 cm. The lateral grooves are close together at their origin from the peri-pallial groove. Colour usually dull greyish-yellow, with a pale sole and foot fringe.

Shell (Text-fig. 1 B)

Measures about 7 × 5 mm, convexly auriform, triangular ; brown periostracum usually much abraded. Columella usually slightly truncate anteriorly, and expanded to a rounded callus posteriorly.

External variation

In var. *trigona* Gassies & Fischer (1856) the shell is thicker and the right margin expanded, in var. *major* G. & F. the shell is larger (11·5 × 7 mm). The body is yellow in var. *flavescens* Moquin-Tandon (1855), and whitish in var. *albina* Moquin-Tandon.

Pallial organs

As in *T. maugei*.

Retractor muscles

The cephalic retractor muscles arise symmetrically on each side of the body-wall about two-thirds of the way back, and not from the left side only as in *T. maugei*. The long, slender penial retractor arises dorsally at the hind end of the body.

Nervous system

As in *T. maugei*.

Radula (Text-fig. 2 B)

The median tooth is vestigial or absent. On each side, eighteen barbed aculeate teeth gradually enlarge up to the penultimate one, while the eighteenth is shorter. The lateral apophysis is nearly midway between base and apex (especially towards the margin of the radula), while in *T. scutulum* it is nearer the basal end. There are about fifty V-shaped rows.

Alimentary system

The large buccal bulb is longer than in *T. maugei* and has, in addition to the bundle of posterior muscles attached to the diaphragm, a series of ten to fifteen pairs of lateral muscles attached to the posterior half of the bulb and arising from the left body-wall. The relations of the liver lobes, intestine and rectum are as in *T. maugei*.

Reproductive system (Text-fig. 1 B)

Compared with *T. maugei*, the central portion of the hermaphrodite duct is longer and more folded, the penis is slighly enlarged at the entrance of the vas deferens, and opposite this point there is a short blunt caecum. There is also a flagellum, which varies in length but may be two-thirds as long as the penis, from the apex of which a long slender retractor muscle runs to the diaphragm at the posterior end of the body. There is no penial papilla, and the mucous membrane is papillate. The spermatheca duct is short, wide and bulbous with the mucous membrane strongly folded longitudinally, and the sac is oval.

Mating, Development, Behaviour, Ecology

See pp. 108–110. The eggs measure 7 × 4 mm, and so are considerably larger than those of *T. scutulum*.

Distribution (Map 2)

T. haliotidea is the most widely distributed species, ranging from the Atlantic isles to the Balkans, and from the North African coast to south Scotland. It probably occurs in every county in Britain up to Stirling, and in the south-eastern and southern counties of Ireland.

Fossil record

Holocene and Recent.

Material examined

Living specimens from Henley-on-Thames, Bedford and Cambridge. Spirit material from Britain, France and Majorca.

Testacella scutulum Sowerby, 1820

Testacella scutulum Sowerby, 1820 : pl. 159, figs. 3–6. Kennington Road, Lambeth, Surrey.

Notes

Taylor (1902–07) considers *T. bisulcata* Risso (1826) as a variety of this species. Plate (1891) and Hoffman (1925), however, consider it to be quite distinct. Plate's figure, copied by Hoffman, shows a flagellum from the anterior end of the penis, and a tubular connection from the vagina to the apex of the flagellum. This most unusual arrangement is said to be confirmed by serial sections.

First British record

By Sowerby (1820).

Diagnostic features

Resembles *T. haliotidea,* but differs in the following. Shell smaller (6 × 3·5 mm) and flatter ; animal yellow in colour, speckled with brown. Apophyses of marginal radular teeth more basal. Penis lacks caecum and flagellum ; free oviduct shorter than vagina ; spermatheca duct longer and narrower (but quite different from that of *T. maugei*).

External appearance

Length when extended, 8–12 cm. The lateral grooves are said to be confluent for about 1 mm at their origin from the peri-pallial groove, but this does not seem to be constant. Colour some shade of yellow, more or less sprinkled with brown ; sole and foot fringe brighter yellow.

Shell (Text-fig. 1 C)

Smaller than that of *T. haliotidea* (6 × 3·5 mm), and flatter—sometimes even concave. The brown periostracum tends to be retained better than in the other species. The columella is slightly truncate anteriorly and expanded posteriorly, as in *T. haliotidea.* Young shells of these two species can easily be confused.

External variation

Most of the varieties mentioned by Taylor (1902–07) refer to continental forms, which may or may not be conspecific with *T. scutulum.* However, var. *aurea* Cockerell (1885) presumably refers to this species : it is orange-coloured, with brown mottling and a bright orange foot sole.

Pallial organs

As in *T. maugei* and *T. haliotidea.*

Retractor muscles

The cephalic retractors arise symmetrically from the body-wall about half-way back. The penial retractor arises far back, from the diaphragm.

Nervous system

As in *T. maugei* and *T. haliotidea.*

Radula (Text-fig. 2 c)

As in *T. haliotidea,* the median tooth is absent and there are eighteen teeth on each side of the mid-line ; but in the outer marginal teeth the apophyses are nearer the bases. There are about forty-five V-shaped rows.

Alimentary system

The buccal bulb has three or four strong muscles from the diaphragm to its posterior end, and the hinder half has five to ten pairs of lateral muscles attached to the left body-wall. The relations of the liver lobes, intestine and rectum are as in *T. maugei* and *T. haliotidea.*

Reproductive system (Text-fig. 1 c)

The ovotestis, albumen gland, prostate and oviduct resemble those of *T. haliotidea,* but the free oviduct is relatively shorter and the vagina longer. The spermatheca duct is intermediate in length and breadth between those of *T. haliotidea* and *T. maugei.* The penis is cylindrical, without dilatations or flagellum, and the retractor muscle arises far back from the diaphragm. The penial mucous membrane is papillate, and that of the spermatheca thrown into longitudinal folds.

Mating, Development, Behaviour, Ecology

See pp. 108–110. The eggs are smaller (4 × 3 mm) than those of the other species, but otherwise similar.

Distribution (Map 3)

Taylor (1902–07 : 18) apparently treated *T. bisulcata* Risso (1826) as a variety of *T. scutulum,* so that his account of the latter's continental distribution is unreliable. In the British Isles, its distribution is almost the same as that of *T. haliotidea.*

Fossil record

Recent.

Material examined

Living specimens from Bedford. Spirit material from Britain and Corsica.

Superfamily ENDODONTACEA

Shell spiral depressed, or reduced to a flat plate or mass of granules enclosed by the mantle. A supra-pedal groove is present, and a caudal mucus gland may be present or absent. The jaw is either crescentic and ribbed, or plaited. Marginal radular teeth generally aculeate. The genitalia are simple.

Family ARIONIDAE

Slug-like animals with the mantle covering only the anterior part of the body, with the respiratory orifice in a slit on the right margin. Shell an oval plate or mass of granules except in *Binneya*, where it is exposed and spiral. The sole is uniform or tripartite. The kidney surrounds the pericardium. An epiphallus is present. The jaw is ribbed (odontognath), the central radular tooth tricuspid, lateral teeth bicuspid, marginals with short wide basal plates, with long mesocones and with or without ectocones.

The Arionidae require relatively high humidity, and dry barren areas are barriers to their dispersal. The family seems to have been derived from Endodontid stock with spiral shells, the cephalic and buccal retractor muscles with a common origin from the columella, and a penial papilla. In the primitive North American genus *Binneya*, the visceral hump is capped by a spiral *Vitrina*-like shell, the tail is solid and the retractors have a common origin. Various genera show transitions from this snail-like condition to that of the most modified subfamily, the Arioninae of the western Palaearctic Region. For a discussion of the probable evolution of the other subfamilies and genera, see Pilsbry (1948 : 660–665).

Subfamily ARIONINAE

Slugs with a wide foot fringe ; caudal mucus gland present ; the shell is reduced to a flattened plate in *Geomalacus*, and to discrete granules in *Arion*. The cephalic retractor muscles are widely separated at their origin from the posterior border of the diaphragm. The stomach apex lies behind the posterior loop of the intestine. The ovotestis lies behind all the intestinal loops. There is no penis or vagina, and the oviduct, spermatheca and epiphallus enter the upper atrium separately.

Of the British genera, *Geomalacus* with its solid shell, anterior reproductive orifice, narrower foot fringe, and extreme western distribution, seems to be the more primitive.

Genus ***GEOMALACUS*** Allman, 1843

Type species *Geomalacus maculosus* Allman, 1843.

Genital orifice below and behind the right upper tentacle ; atrium greatly elongated ; genital retractor muscle arising from the dorsal body-wall at the extreme posterior end of the body and inserted into the spermatheca duct ; shell a compact oval calcareous mass.

G. maculosus is the only member of this genus occurring in the British Isles, though one or two more are found with it in the Iberian peninsula.

Geomalacus maculosus Allman, 1843

Geomalacus maculosus Allman, 1843 : 851. Lough Caragh, Co. Kerry, Ireland.

Notes

The types were found by W. Andrews of Dublin in 1842.

First British record

By Allman (1843).

Diagnostic features

Distinguished from species of *Arion*, externally by the anterior situation of the reproductive orifice, narrower median area of the sole, and maculate colour pattern ; and internally by the solid oval shell, greatly elongated atrium, and long genital retractor arising far back from the mid-dorsal line of the body-wall.

External appearance (Pl. 1, fig. 1)

Length when extended about 5·5 cm, but occasionally up to 9 cm. The granulose mantle occupies about one-third of the body, with the respiratory orifice a little in front of the centre of the right border. The reproductive orifice is nearer to the right upper tentacle than to the respiratory orifice. The supra-pedal groove is deep and distinct and the pedal groove indistinct. The caudal mucus gland is a transverse slit. The body shows about twenty-five rows of polygonal tubercles (Text-fig. 3 C). The colour is grey, brown or nearly black, irregularly marked with yellow or white maculations more or less developed. The young have two longitudinal bands on each side, which tend to become obscured in the adult, but sometimes remain. In contrast to *Arion*, *Geomalacus* sometimes rolls up like the woodlouse *Armadillidium*.

External variation

Var. *fasciata* Cockerell (1892) retains the banding characteristic of the young—animal white or whitish with black or brown markings : mantle with dark marbling and lateral bands, body with a dark subdorsal band along each side. Charles Oldham bred in captivity a crimson form, var. *rutilans* Oldham (1942*b*), which has not been observed in the wild. The other varieties depend merely on the relative development of dark pigment on a pale ground : var. *allmani* Heynemann (1873), dark brown or grey with whitish maculations ; var. *verkruzeni* Heynemann, grey, darker dorsally, with whitish maculations ; var. *andrewsi* Mabille (1867), whitish, overspread with blackish spots.

Shell (Text-fig. 3 I)

Variable, but usually solid, oval, convex above and concave below, measuring about 4 × 3 mm.

Pallial organs (Text-fig. 3 B)

The kidney completely surrounds the pericardium, and the cavity is occupied by lamelliform folds. The ventricle lies behind the auricle. The anterior branch of the aorta follows the usual course, arching over and passing beneath the anterior intestinal loop, and running forwards between the visceral and pedal ganglia to supply the anterior end of the body. The posterior aorta runs backwards to the digestive and genital systems.

Retractor muscles (Text-fig. 3 B)

The right and left cephalic retractor muscles are widely separated at their origin from the diaphragm, behind the kidney. The buccal retractor arises from the dorsal body-wall, a little further back and slightly to the right of the middle line. The right tentacular branch lies to the left of the oviduct and epiphallus, and does not pass between them.

Nervous system

The cerebral commissure is of medium length. The cerebral ganglia give rise to nerves to the head and lips, the peritentacular nerves, the combined ocular and olfactory nerve, the nerve to the lower tentacle, and on the right side to the genital nerve supplying the epiphallus and vas deferens. The right pleural, visceral and abdominal ganglia are fused together, but just distinguishable, and the same is true of the left pleural and the left visceral ganglia. The pleuro-pedal commissures are very short. The buccal ganglia, as well as supplying the buccal bulb, send a nerve to the salivary glands.

Jaw (Text-fig. 3 D)

The jaw is about 3 mm across, dark brown, arcuate, and crossed by eight or ten broad ribs which slightly denticulate the upper and lower margins. The number of ribs may be reduced by fusion, and there is sometimes a slight median projection.

Radula (Text-fig. 3 E)

The radula is about 8 mm long. There are usually about 200 rows of teeth, but the number varies considerably. The central tooth has very small ectocones. The lateral teeth, about twenty in number, have a large mesocone, a small ectocone, and no endocone. The ectocone gets smaller in the outer lateral teeth. In the marginal teeth it descends to the base of the mesocone, and gets larger again as the margin of the radula is approached.

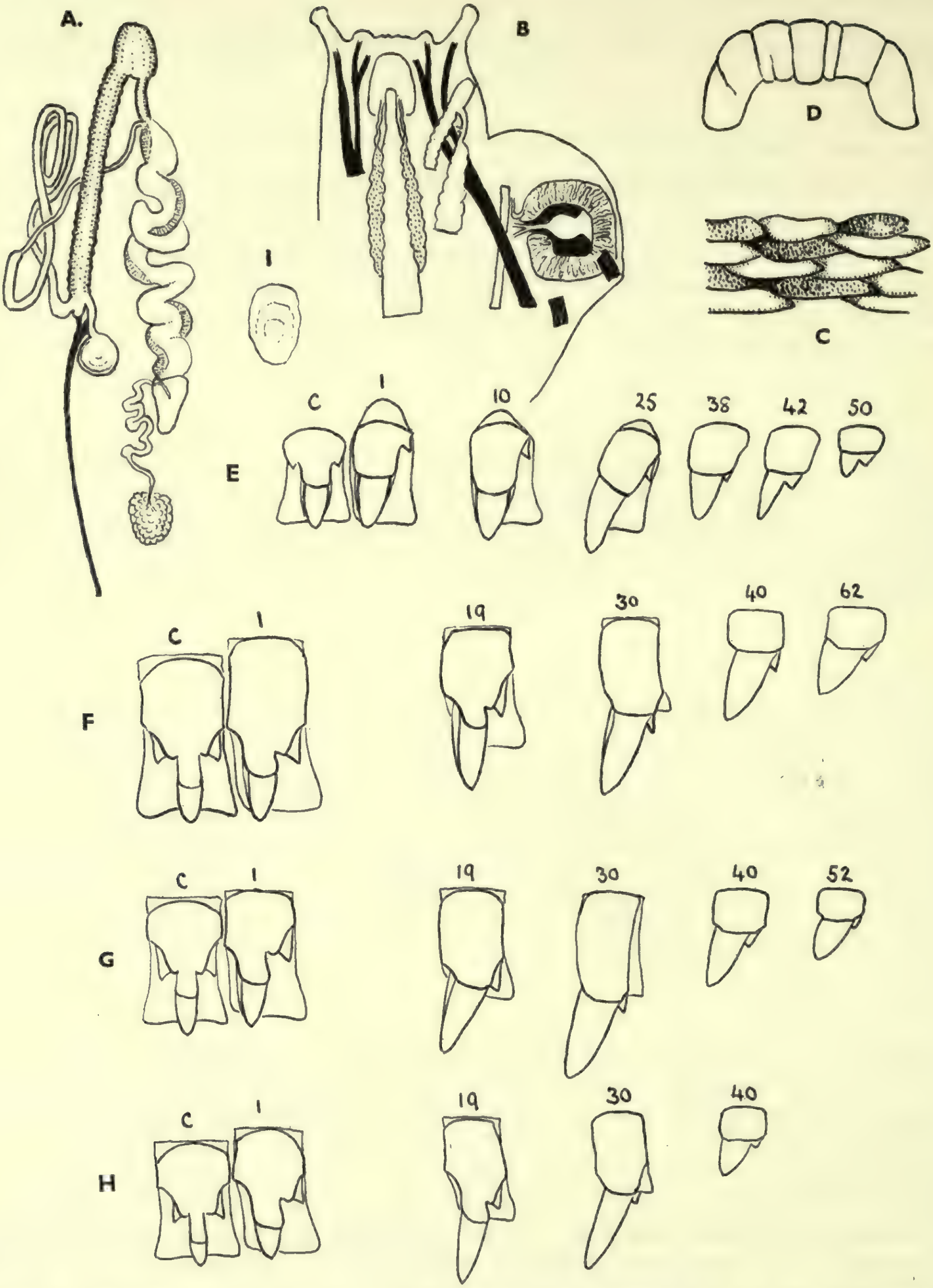
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FIG. 3. *Geomalacus maculosus*. **A**. Reproductive organs (× 2·7). **B**. Head and mantle region (× 1·7) with mantle reflected to the right showing kidney, pericardium, rectum, terminations of genital and alimentary systems, origin of pharyngeal and left ocular retractors cut short. **C**. Polygonal body-tubercles. **D**. Jaw (× 13). **E**. Representative radular teeth (× 330). **I**. Shell.

Arion. Representative radular teeth (× 330). **F**. *A. ater*. **G**. *A. lusitanicus*. **H**. *A. subfuscus*.

Alimentary system

The oesophagus, after passing through the nerve ring, enlarges to a crop, merging into the stomach which forms the most posterior part of the alimentary canal. The narrower intestine passes far forwards (to the level of the kidney) and then turns back, but does not reach the stomach before it runs forwards again, as the rectum, to end in the anus in the posterior lip of the respiratory orifice. The short ducts of the anterior and posterior lobes of the liver open at the junction of stomach and intestine.

Reproductive system (Text-fig. 3 A)

The somewhat raspberry-shaped brown ovotestis lies between the upper and lower lobes of the liver, at the apex of the stomach. The pale hermaphrodite duct passes forwards, becoming wider and folded, towards the linguiform albumen gland. It then becomes narrower, runs backwards between the lobes of the albumen gland, and turns sharply forwards, forming a " claw " or seminal vesicle. The common duct is much folded, the prostatic portion showing as a yellow ribbon. The narrower free oviduct enters the lower end of the atrium ; its mucous membrane is thrown into fine longitudinal folds. The lower atrium shows internally a complicated mass of large sinuous folds, and is also remarkable in having a long slender diverticulum with circular folds, extending backwards as far as the albumen gland. The short duct of the globular spermatheca enters the apex of this diverticulum. The vas deferens runs backwards from the free oviduct towards the apex of the atrial diverticulum, to enter the wider epiphallus which is very long and much coiled, the coils being bound together by connective tissue. The epiphallus enters the atrial diverticulum close to the spermatheca duct. A long slender retractor muscle, arising from the mid-dorsal line at the posterior end of the body, is inserted at the neck of the spermatheca and apex of the diverticulum. The mucous membrane of the epiphallus shows longitudinal rows of papillae, and that of the spermatheca longitudinal folds. A membrane with a series of muscular bands extends from the atrial diverticulum to the diaphragm, and similar bands from the lower atrium to the body-wall.

Mating

This has not been recorded.

Development

The ellipsoidal eggs are said (Taylor, 1902–07 : 256) to be relatively large, from 8·5 × 4·25 to 6 × 4 mm, and to be white when laid, turning brown. They are laid, in clusters of from 18 to 24, in July and August, and hatch in from six to eight weeks. The young, which mature in the following summer, show two dark bands on each side which fade during growth.

Behaviour

When irritated, it can roll up like the woodlouse *Armadillidium* (Taylor, 1902–07 : 257).

Ecology

G. maculosus lives on the bare mountain slopes of Old Red Sandstone in Cork and Kerry, where it browses on the algae, mosses and liverworts which coat the boulders. In captivity it readily feeds on lettuce and carrot, and has been observed to attack small snails such as *Vitrina pellucida.*

Distribution (Map 4)

Portugal, north-western Spain, and Vennes (France). In Britain it is confined to south-western Ireland, in the counties of Cork and Kerry.

Fossil record

Recent.

Material examined

Preserved specimens from Glengariff, Co. Cork (August 1931), and other localities in Cork and Kerry.

Genus ***ARION*** Férussac, 1819

Type species *Arion empiricorum* Férussac (= *Limax ater* Linnaeus, 1758).

The diagnostic features of the genus are those of the subfamily Arioninae. Differences from *Geomalacus* are: reproductive orifice immediately below posterior lip of respiratory orifice; upper atrium not prolonged backwards as a diverticulum; genital retractor short, arising from diaphragm close to left cephalic retractor, and inserted into both spermatheca duct and free oviduct; shell reduced to discrete granules; median area of sole wider.

A. intermedius and *A. fasciatus* seem to be less advanced than the other species, in the absence of a ligula, the limited eversion of the gentalia during coitus (in *A. fasciatus* at least), and the slightly more anterior position of the reproductive orifice in *A. fasciatus. A. hortensis* differs strikingly from *A. fasciatus* and from the larger species, but agrees with *A. subfuscus* and *A. lusitanicus*, in having the ligula (or its functional equivalent) in the proximal part of the oviduct. *A. lusitanicus* is in some respects intermediate between *A. subfuscus* and *A. ater*; while the latter, in which the banding pattern disappears completely in the adults, is probably the least primitive.

The various subgenera and sections that have been proposed are not satisfactorily delimited. Hesse (1926 : 64–69) uses the following subgenera: *Lochea* Moquin-Tandon (1855), for *A. ater* and *A. lusitanicus* (though the genitalia of the latter are much more like those of *A. subfuscus*); *Mesarion* Hesse, for *A. subfuscus*; *Carinarion* Hesse, for *A. fasciatus*; *Kobeltia* Siebert (1873), for *A. hortensis*; and *Microarion* Hesse, for *A. intermedius.*

Arion intermedius Normand, 1852

Arion intermedius Normand, 1852 : 6. Valenciennes.
Arion minimus Simroth, 1885 : 237, pl. 7, fig. 41.

First British record

By Alder (1848 : 124), as *Arion flavus*.

Diagnostic features

Small size, tubercles assume a conical shape with translucent apices when animal contracts, yellow mucus accumulates at each end of foot ; reproductive orifice slightly anterior to respiratory orifice.

External appearance (Pl. 1, fig. 7)

This is the smallest British Arionid, about 2 cm long when crawling. Its colour varies from yellow to some shade of grey, with the head darker grey or black, and there may or may not be body and mantle bands. All these colour varieties may be found living together. *A. intermedius* is easily distinguished from the young of larger species by the form of its tubercles, which stand up in little conical eminences with translucent tips when the animal contracts—hence the popular name Hedgehog Slug. The pair of mantle bands together form a lyre-shaped figure, and the right band arches over the respiratory orifice and sends a branch down below and behind it. The sides of the body are paler than the back, the foot fringe is yellowish-grey, and just above it there is a row of black dots towards the anterior end. The sole is yellowish-grey, and yellow mucus tends to accumulate at each end of it. The genital orifice is immediately below the slit of the respiratory orifice, and thus is further back than in *A. fasciatus* but slightly further forward than in the other species.

External variation

Var. *normalis* Moquin-Tandon (1855), yellow with blackish head and tentacles ; var. *plumbea* Collinge (1892*b*), dark grey ; var. *brunnea* Taylor (1902–07), maroon-brown with darker bands ; var. *alba* Taylor, almost white.

Shell

The shell granules are not specifically distinguishable. In calcareous sites they may be aggregated into an irregular mass.

Pallial organs

As in *A. ater* (p. 139).

Retractor muscles

As in *A. ater*, except that the cephalic retractors do not arise at the same level, but with the right a little further forward than the left ; while the genital retractor sends a branch to the junction of oviduct and atrium, as well as to the neck of the spermatheca.

Nervous system

As in *A. ater.*

Jaw

About 1 mm across, arcuate and crossed by seven to ten widely-spaced ribs. Of the usual Arionid shape, and so not like Taylor's figure (1902–07, fig. 248).

Radula

About 2 mm long, with about 120 transverse rows of teeth. The base of the mesocone of the central tooth is more constricted than in the other species. There are about sixteen lateral and sixteen marginal teeth, each with mesocone and ectocone : they do not have endocones. Formula C.16.16 × 120.

Alimentary system

As in *A. ater,* except that the visceral mass is less twisted.

Reproductive system (Text-fig. 4 H)

The deeply pigmented ovotestis lies between the lobes of the liver, and is partly exposed on the surface of the visceral mass. The central part of the pale hermaphrodite duct is wider and somewhat sinuous, then narrows and runs back on the short linguiform albumen gland and bends sharply forwards, making a " claw " or seminal vesicle. The sperm-oviduct is short, and the free oviduct enters the very short upper atrium without a ligula. The mucous membrane is thrown into five or six low longitudinal folds. The lower atrium is about 2 mm long and smooth internally. The spherical spermatheca is connected to the upper atrium by a very short duct, much dilated at its base. The vas deferens is about 2 mm long, and the epiphallus about the same length.

Spermatophore

Unknown.

Mating

Not recorded.

Development

The ellipsoidal eggs are relatively large (2 × 1·5 to 2 × 2 mm), opaque, white and dotted with calcareous spots. They are laid in the summer and autumn, and hatch in about three weeks. The young at birth are 4 mm long, and easily recognizable as miniatures of the adults.

Ecology

Common in the moist ground-litter of woods and copses, beneath logs, and at the roots of grass in open fields. Often found feeding on toadstools in the wild, and in captivity readily eats carrot, lettuce and oatmeal.

Distribution (Map 5)

Portugal, Spain, France, northern Italy, Switzerland, Germany, Scandinavia, Russia, Azores (and introduced into New Zealand, Polynesia and North America). It probably occurs in every vice-county in the British Isles, including islands northwards to the Orkneys and Shetland.

Fossil record

Although shell granules of *Arion* are not recognizable with certainty, they are recorded from the Cromerian onwards. They cannot be assigned specifically.

Material examined

Living specimens from many parts of England and Wales. Spirit material from Britain, France, Norway and Tahiti.

Arion fasciatus (Nilsson, 1822)

Limax fasciatus Nilsson, 1822 : 4. ? Sweden.
Arion circumscriptus Johnston, 1828 : 76.

Notes

Collinge (1892*b*) reinstated Nilsson's name, though it has not been adopted by other British authors. Lohmander (1937) also concluded that *fasciatus* is the valid name, though he continued to use *circumscriptus*. Nilsson's description of his species leaves no doubt that it is the *A. circumscriptus* of most authors, and Collinge's use of *fasciatus* prevents any action being taken to conserve *circumscriptus*.

First British record

By Johnston (1828).

Diagnostic features

Body bell-shaped in transverse section when contracted, mid-dorsal line of tubercles pale and raised, reproductive orifice in front of respiratory orifice, right mantle band arches over respiratory orifice, sole opaque porcelain white ; spermatheca with short stout duct and long tapered sac, spermatophore coiled anteriorly.

External appearance (Pl. 1, fig. 5)

Length when crawling about 3–3·5 cm. Easily distinguished from *A. hortensis* by the opaque white sole, and by the bell-shaped transverse section of the body when contracted (caused by splaying-out of the lower part). The reproductive orifice is further forward than in our other species, being a little in front of the slit of the respiratory orifice. Body and mantle some shade of grey, becoming paler towards the foot and with a dark lateral band on each side. The mantle bands form a lyre-shaped figure, and the right band arches over the respiratory orifice without sending a branch below it. The bands are set at a higher level than in *A. hortensis*. The tubercles of the mid-dorsal line are larger and paler than those on each side, forming a keel (hence the sectional name *Carinarion* Hesse, applied to this species) : this is often more distinct in the young. The foot fringe is somewhat lineolated, especially towards the tail.

External variation

Var. *grisea* Collinge (1892*c*), light silver-grey with dark bands ; var. *flavescens* Collinge (1892*a*) (= var. *circumscripta* Økland, 1923), light brownish-yellow, with dark bands and a yellow zone over the foot. Lohmander (1937) discusses whether these and other named forms are varieties or subspecies.

Pallial organs

As in *A. ater*.

Retractor muscles

The genital retractor is mainly inserted into the duct of the spermatheca, but usually sends a small branch into the middle of the free oviduct. Otherwise as in *A. ater*.

Nervous system

As in *A. ater*.

Jaw

Of the usual arcuate shape, crossed by ten to twelve ribs ; about 1·25 mm across, coloured yellow to pale brown.

Radula

Closely resembles that of *A. hortensis*, but the marginals often have the small ectocone better developed. Length 3–4 mm, formula C.11.23 × 120.

Alimentary system

As in *A. ater*, except that the visceral mass is less twisted.

Reproductive system (Text-fig. 4 I)

The ovotestis is darkly pigmented, the hermaphrodite duct has the usual " claw " or seminal vesicle at its entry into the albumen gland, and the sperm-oviduct is pinkish in colour, with a broad yellow prostatic ribbon. The free oviduct is rather long and slender, agreeing with that of *A. intermedius* in not being dilated terminally to contain a ligula as in *A. hortensis*. The spermatheca has a short stout duct and an elongated sac, wide at the base and tapering apically. It varies a good deal, sometimes assuming bizarre shapes. The vas deferens is about the same length as the epiphallus, which terminates with a slightly marked annular swelling. The upper atrium is very small, and contains no ligula. The lower atrium is long, dorso-ventrally flattened, and yellow.

Spermatophore (Text-fig. 4 G)

A chitinous tube about 4 mm long, with five low ridges of which the most prominent is finely toothed. Within the spermatheca, the spermatophore is bent into a U, and is swollen for a short distance behind the slender coiled anterior end. On this swollen part, Lohmander (1937) describes, but does not figure, a small projection which anchors the spermatophore to the mucous membrane of the spermatheca. Økland (1923) figures an incomplete spermatophore, and Lohmander (1937) complete ones.

Mating

Coitus lasts about twenty minutes. In contrast to *A. hortensis*, *A. subfuscus* and *A. ater*, there is little or no eversion of the genitalia.

Development

The ellipsoidal eggs, 3 × 2 mm, are yellow or sometimes dark amber, more flexible and translucent than those of other species of *Arion*. They are laid in clutches of up to thirty, from May to the autumn, and hatch in four or five weeks (or longer in cold weather). The newly-hatched young are 5 mm long, pale yellowish-grey; not darker dorsally, but with a pale central line of larger tubercles forming a keel towards the tail. The lyre-shaped figure formed by the mantle bands is faint in front and darker posteriorly.

Ecology

A. fasciatus is common amongst dead leaves and moss and under logs and stones, in thickets, fields and waste places, and sometimes in gardens.

Distribution (Map 6)

Probably every vice-county of the British Isles, and in Iceland (? introduced), the Faroes, Scandinavia, France, northern Italy, Rumania, western Russia, ? Spain. Introduced into North America.

Material examined

Living from many places in Britain. Spirit material from Britain, France and Italy.

Arion hortensis Férussac, 1819

Arion hortensis Férussac, 1819: 65, pl. 2, figs. 4–6. Presumably France.
Arion elongatus Collinge, 1894 : 66, pl. 5A, figs. 1–4.
Arion coeruleus Collinge, 1897*b* : 444.

First British record

By Gray (1821 : 239).

Diagnostic features

Differs from *A. fasciatus* in the following : body semicircular in transverse section when contracted, no enlarged mid-dorsal tubercles, reproductive orifice further back, mantle band surrounds respiratory orifice, sole yellow or orange ; spermatheca globular, free oviduct longer and proximally more slender, spermatophore hooked posteriorly and either discoidal or pointed anteriorly, brown patch on buccal bulb.

External appearance (Pl. 1, fig. 4)

Length extended 2·5–3 cm. When contracted, the body is semicircular, not bell-shaped, in transverse section. The reproductive orifice is below the posterior lip of the respiratory orifice. The dark brown or black back is sprinkled with yellowish-brown dots, giving a pepper-and-salt appearance, the sole is pale yellow to bright orange, and the mucus is yellow. In alcohol, the back becomes bluish-grey and the sole loses its orange colour. The lateral bands are placed lower on the body than in *A. fasciatus*, and run along the edges of the mantle, surrounding the respiratory orifice instead of arching over it.

External variation

Var. *grisea* Moquin-Tandon (1855), pale grey and bandless ; var. *nigra* Moquin-Tandon, bands nearly obliterated by general dark pigmentation ; var. *rufescens* Moquin-Tandon, reddish with black bands ; var. *caerulea* Collinge (1892*a*), bluish with dark bands, and yellow sides.

Pallial organs

As in *A. ater.*

Retractor muscles

As in *A. fasciatus.*

Nervous system

As in *A. ater.*

Jaw (Text-fig. 7 G)

About 1 mm across, doubtfully distinct from that of *A. fasciatus.*

Radula

Similar to that of *A. fasciatus*, but the ectocone of the marginal teeth is less frequently present. Formula C.11.24 × 100.

Alimentary system (Text-fig. 4 A)

Visceral mass less twisted than in *A. ater*. The buccal bulb has a brown shield-shaped mark on the upper surface—an apparently good specific character not recorded in the literature.

Reproductive system (Text-figs. 4 B and C)

The very darkly pigmented ovotestis lies over the apex of the stomach, near the posterior end of the visceral mass, and is largely exposed on the surface. The middle dilated portion of the hermaphrodite duct is much folded, yellowish-white, and the terminal slender part shows the usual " claw " or seminal vesicle where it enters the elongated albumen gland. The sperm-oviduct is pale pinkish-brown, with a conspicuous yellow ribbon-like prostate. The free oviduct is unusually long and slender proximally, and dilated distally before entering the small white upper atrium. The vas deferens is short, and the epiphallus about the same length. The spermatheca duct is short and stout, with a bulbous base, and the sac is spherical. The lower atrium is yellow, with a soft glandular covering.

As in *A. fasciatus* and *A. intermedius*, there is no ligula in the upper atrium. However, within the dilated distal end of the oviduct (Text-fig. 4 C), two conspicuous longitudinal folds correspond functionally with this structure during coitus (Quick, 1946). Below the termination of the spermatheca duct is a region of thickened mucous membrane in the atrium. In the slugs observed in Swansea (see below), the entering spermatophore adhered to this region. The epiphallus terminates in a short papillate papilla, which is very conspicuous when the atria are everted in coitus (Text-fig. 4 E).

Both British and Dutch slugs show some variation in the folds of the oviduct representing the ligula, and in the relative length and thickness of the firm cartilaginous part ; but these differences could be due to differences in the degree of maturity of the animals, and to the extent of contraction during fixation in alcohol.

Spermatophore (Text-figs. 4 F and M)

Two types of spermatophore have been found in slugs from different localities. Since the spermatophores of *Arion* are seldom seen, it seems better to regard the slugs bearing the two types as varieties or local races, rather than as distinct species, until further anatomical or ecological differences are demonstrated.

Slugs from Reading and from Zaandam in Holland (collected by Mr. D. Aten) have spermatophores in the form of simple chitinous tubes, 6·5 mm long, recurved at the slender posterior end and slightly shouldered near the anterior end, smooth and without denticulation (Text-fig. 4 F).

Slugs from a garden in Eaton Crescent, Swansea (Glamorgan), which otherwise agree with those from Reading, have the very different spermatophores described by Quick (1946). These are 5 mm long, shaped like cloves, with the anterior end forming a flattened disc with a crenulated edge, and with a ridge carrying about fifty-six forwardly pointing denticulations running the whole length of the convex side (Text-fig. 4 M).

Mating (Text-fig. 4 D)

Mating occurs in April and December, and probably in other months. After the usual " following " and licking of mucus, slugs from Swansea (spermatophores as in Text-fig. 4 M) curve in a semicircle head to head, and the atria are everted as a translucent mass with the lower atria stretched to a narrow yellow ring and the lower atria in contact. A long slender mobile club-shaped process is everted, which plays over the partner's body in the same manner as the sarcobelum of *Agriolimax.* However, subsequent dissection shows it to be the everted slender proximal part of the oviduct, functioning as a stimulatory organ, a modification which appears to be unique (Text-fig. 4 E).

Coitus in Swansea slugs lasts for about an hour and a half. Gerhardt (1935) describes the mating of *A. hortensis* as lasting only twenty-five minutes, and the everted masses as small and featureless, in slugs whose spermatophores lacked serrations. This suggests that more than one species may be involved, though Mr. D. Aten (*in litt.*) states that the Zaandam slugs, having smooth spermatophores, evert their oviducts in coitus.

Development

The opaque yellow, sticky eggs measure 2·5 × 2 mm, and are laid in clusters of up to thirty. A second and third clutch may follow at three-weekly intervals. In the winter, the eggs take six or seven weeks to hatch. The newly hatched young are 4 or 5 mm long, and differ from those of *A. fasciatus* in having a darker dorsum and central mantle area. The usual body bands and lyriform mantle bands are present, and there is no dorsal line of pale conspicuous tubercles. The tentacles are violet-brown.

Ecology

This species is very common in gardens, allotments and fields, and burrows in the ground more than the other species of *Arion*. It can become a serious pest, by eating carrot, potato, etc. It is also frequent in woodland under logs and débris.

Distribution (Map 7)

Every county in the British Isles ; Scandinavia and western Europe to western Russia, (North Africa). Introduced into North America.

Material examined

Living and in spirit from many places in England and Wales, and from Zaandam, Holland.

Arion subfuscus (Draparnaud, 1805)

Limax subfuscus Draparnaud, 1805 : 125, pl. 9, fig. 8. France.
Arion fuscatus Férussac, 1819 : 65, pl. 2, fig. 7.

First British record

Possibly by Johnston (1838), as *Arion subflavus* (a nomen nudum). Up to about 1880, however, *A. subfuscus* was generally considered as a variety of *A. ater.*

Diagnostic features

Adults larger (6–7 cm) than *A. fasciatus* and *A. hortensis*, smaller than *A. lusitanicus* and *A. ater* ; differ from young of large species in smaller tubercles, narrower foot fringe, inability to contract to hemispherical shape. Internally differs from *A. hortensis* in relatively shorter proximal, slender, part of free oviduct, longer spermatheca duct.

External appearance (Pl. 1, fig. 2)

Length extended, from 5 to 7 cm. The colour is usually yellowish-brown, darker on the dorsum and head and on the body bands. On the mantle the right band completely surrounds the respiratory orifice. The foot fringe is yellowish and lineolated more or less distinctly with black, and the sole is pale yellow, sprinkled with whitish specks, and obscurely tripartite. The mucus, especially on the mantle, is yellow or orange. When contracted, *A. subfuscus* neither assumes the hemispherical shape nor exhibits the rolling reflex (p. 145) of *A. ater.*

External variation

This as usual depends on the relative development of black, red and yellow pigment, and the distinctness of the bands : var. *rufofusca* Draparnaud (1805), rufous with black bands ; var. *bicolor* Moquin-Tandon (1855), red with darker dorsum and no bands, foot fringe orange ; var. *fuliginea* Morelet (1845), dark brown, fringe yellowish; var. *nigricans* Pollonera (1887*b*), black ; var. *cinereofusca* Draparnaud (1805), ashy grey ; var. *succinea* Bouillet (1835), yellow or orange ; var. *pegorarii* Lessona & Pollonera (1882), quadrifasciate ; var. *alba* Esmark (1883), whitish. In most cases, the yellow pigment is largely contained in the mucus, and when this is removed the animal becomes brown or grey, as do alcohol specimens.

Pallial organs, retractor muscles, nervous system

As in *A. ater.*

Jaw

Brown, arcuate, about 1·5 mm across, with from ten to sixteen transverse ribs.

Radula (Text-fig. 3 H)

About 4·5 × 2 mm. About ten more teeth on each side of each row than in *A. hortensis*. Formula C.15.30 × 140.

Alimentary system

Similar to that of the other species of *Arion*, except that the visceral mass is rather more twisted than in *A. intermedius* and *A. fasciatus*, and less so than in *A. ater*.

Reproductive system (Text-figs. 6 D and F)

From the pale brown ovotestis, the greatly convoluted white hermaphrodite duct enters the albumen gland, with the usual " claw " or seminal vesicle. The common duct is voluminous and folded, the male or prostatic portion yellow and the female part pinkish-grey. The first part of the free oviduct is short and slender, and the longer distal part dilated. This part contains two prominent longitudinal folds of mucous membrane forming the ligula as in *A. hortensis*. The spermatheca duct is bulbous at its origin, then longer and more slender than in *A. hortensis*, and ends in a larger spherical spermatheca sac. The vas deferens and epiphallus are very similar to those of *A. hortensis*, but the terminal annular thickening is more pronounced. The upper atrium is small, the yellow glandular lower atrium of medium size with a wrinkled mucous membrane.

Spermatophore (Text-fig. 6 G)

Very different from that of *A. hortensis* : about 20 mm long, slender anteriorly, then dilating, to taper again to an almost filamentous tail. The convex edge is finely denticulate.

Mating

Mating occurs in March, April and May, and perhaps other months. One of a pair follows the other for about half an hour, " licking " the caudal mucus. Then they curve around in a semicircle with the right side of the necks in contact. In about fifteen minutes the lower atria are everted as small yellow eminences. These rapidly enlarge as eversion is completed, and the combined atria form an ovoid bluish-white mass between the two animals, the junction of the two atria being barely visible as a fine line. After three-quarters of an hour the mass shrinks and the animals separate, and the spermatophores are momentarily visible, partly protruding from the spermatheca ducts as the remainder of the shrinking mass is withdrawn. For further details see Quick (1946). The slender portion of the free oviduct is not everted as a stimulator as it is in *A. hortensis*, where this portion of the oviduct is longer. The combined mass resembles that of *A. ater*, since the differing situation of the ligula does not affect the aspect.

Development

The opaque leathery eggs, measuring from 2·25 × 2·25 to 3·25 × 2·25 mm, vary considerably in size and shape, even in the same cluster. Eggs are laid three weeks after mating. They are laid in masses of up to fifty, and tend to adhere together, several eggs sometimes being enclosed in a common tubular coat of mucus. They are white at first and become yellow or brown. Hatching occurs in from three to five weeks. The newly hatched young are about 6 mm long, grey, with darker dorsal region, and with lateral body and mantle bands. The tentacles are violet. Newly hatched *A. ater* are orange, straw colour or pale greenish-grey, and the tentacles dark grey rather than violet ; but the most notable difference is that the anterior ends of the mantle bands are closer together than in *A. subfuscus* (Pl. 1, figs. 9 and 11).

Ecology

A. subfuscus lives under logs and litter in deciduous and coniferous woods, and is one of the few species found in pine woods. It is also frequent in damp hedgerows, waste ground and some gardens. It feeds on the algal and fungal film on logs, and also on the larger fungi. In captivity it readily eats carrot, lettuce, oatmeal and dead slugs (Map 8).

Distribution

The whole of Great Britain and Ireland, except possibly parts of East Anglia and eastern Scotland. Most of Europe, north of a line through Orenburg and Odessa (Russia), northern Italy, Barcelona and Oporto. Introduced into North America.

Material examined

Living from many places in Britain. Spirit material from Britain, France, Luxembourg, Germany, Italy and Madeira.

Arion lusitanicus Mabille, 1868

Arion lusitanicus Mabille, 1868 : 134. La Sierra d'Arriba, near Lisbon.

Notes

The name *lusitanicus* is applied to this species with some hesitation, since Mabille (1868) described the tubercles as " peu allongés ". However, Pollonera's description and figures (1889 : 626, pl. 9) leave little doubt about the identification. *A. nobrei* Pollonera (1889) is similar to *A. lusitanicus* but smaller, with smaller tubercles, completely black, and with the distal genital ducts even more strongly pigmented. A specimen from Portugal in the B.M. (N.H.) collections, identified as *A. nobrei*, agrees with this description.

Cain & Williamson (1958) discuss specimens of *Arion* collected at Nuneaton, Warwickshire, which perhaps suggest that the status of *A. lusitanicus* in Britain may require further investigation.

First British record

By Collinge (1893). Though again recorded by Collinge (1897*a*), the species was overlooked by Taylor (1902–07) and by other authors on the British fauna (e.g. Roebuck, 1921 ; Kennard & Woodward, 1926 ; Ellis, 1926 and 1951 ; Quick, 1949), until its rediscovery in Durham by Mrs. Vincent (Quick, 1952).

Diagnostic features

Large, up to 10 cm in length, with coarse tubercles like *A. ater* ; from which it is internally distinguished by the dilated distal part of the free oviduct, which lodges the ligula. Distinguished from *A. subfuscus* by coarse tubercles and a longer spermatheca duct.

External appearance

The length when crawling is from 7 to 10 cm. The colour varies as in *A. ater*, and may be dark grey, reddish-yellow, brown or dull greenish-grey, with darker head and tentacles. The transversely lineated foot fringe is sometimes darker and sometimes lighter than the body, and the sole is generally pale, but dark in some Nuneaton specimens. The respiratory orifice does not dilate to the same extreme degree as in *A. ater*. In the younger stages there is on each side a dark lateral band (Text-fig. 5 D). On the mantle the bands form a lyre-shaped figure, the right band surrounding the pulmonary orifice on all sides, and anteriorly they are a little closer together than in *A. subfuscus* of similar size. Sometimes the bands are retained up to maturity.

External variation

Var. *rufescens* Collinge (1893), body dark red, sides of body bandless ; var. *nigrescens* Collinge, black or plumbaceous ; var. *olivaceus* Collinge, various shades of olive-green ; var. *flavogriseus* Collinge, yellowish-grey, foot fringe lighter than the body.

Pallial organs, retractor muscles, nervous system

As in *A. ater*.

Jaw

Intermediate in size (3 mm across) between those of *A. subfuscus* and *A. ater* ; arcuate, crossed by from nine to thirteen rather broad even ribs ; pale brown or yellow in light examples, nearly black in dark ones.

Radula (Text-fig. 3 G)

Intermediate in size between those of *A. subfuscus* and *A. ater*. The formula varies (in adult specimens from Durham) between C.17.35 and C.19.45.

Alimentary system

As in *A. ater*.

Reproductive system (Text-figs. 5 A and E)

The very dark ovotestis lies a little further forward than in *A. ater.* The dilated central part of the hermaphrodite duct is folded in a zig-zag manner, and then narrows to form the usual " claw " at the albumen gland, which varies in size with the maturity of the animal. A yellowish-pink fold or ruffle accompanies the first part of the sperm-oviduct. The free oviduct is slender at first, and then becomes greatly enlarged, to narrow again slightly where it enters the upper atrium. This dilated part, in both the Durham and the Nuneaton examples, is deeply pigmented in a characteristic way (Text-fig. 5 A). The spermatheca duct is rather longer than in *A. subfuscus*, somewhat dilated at the origin. It also sometimes shows a slight dilatation, with stronger mucous folds, between the origin and the spherical spermatheca sac. The vas deferens is about as long as the epiphallus, and the latter shows a conspicuous annular ring at its termination. The distal half of the epiphallus is deeply pigmented like the oviduct, the pigment usually tailing off in two tongues. In some individuals this pigmentation is less pronounced. The upper atrium is small, the lower pear-shaped with thick glandular-looking walls, sometimes yellow, and sometimes sprinkled with minute spherical white granules.

The upper atrium contains no ligula, but the distal dilated part of the oviduct contains two conspicuous folds which apparently represent this structure, and function similarly (Text-fig. 5 E). In *A. ater* the ligula occupies the large upper atrium in both young and adult animals. Examination of the genital ducts of immature animals of *A. subfuscus* and *A. lusitanicus* (Text-figs. 6 C and D) shows that the ligula lies in the oviduct, as in the adult, and does not " migrate " upwards or downwards. It is noteworthy that in young *A. ater* the oviducal branch of the genital retractor is inserted as in *A. hortensis*, *A. subfuscus* and *A. lusitanicus* ; while in adult *A. ater* (Text-fig. 6 K) the distal part of the oviduct becomes relatively much shorter, bringing the retractor close to the atrium. It could be argued that the lateral atrial pouch of *A. ater* is homologous with the dilated terminal portion of the oviduct of the other species, or alternatively that this portion of the oviduct is a diverticulum of the atrium. Seeing that this portion is so well devleoped in the early stages of growth, the second alternative is unlikely. There is in *Geomalacus maculosus* a long backward extension of the atrium ; but this carries back the epiphallus and the spermatheca, and does not affect the oviduct.

Spermatophore (Text-figs. 6 H and I)

A chitinous tube 20 mm long, armed with a spiral row of serrations, most prominent towards the anterior end ; and two low smooth ridges at the posterior end, which die out anteriorly.

Mating (Text-fig. 6 E)

The figure shows the appearance of the reproductive organs just before they are withdrawn after mating, with the partner's spermatophore protruding from the spermatheca duct. Observations on the mating of *A. lusitanicus* are too few and incomplete to permit of comparison with the other species.

Development

The white eggs measure about 3 × 3·25 mm, but vary considerably in size and shape, both within and between clusters, and become yellower with age. In the laboratory, they have been laid in January and in March; and in September by laboratory-bred animals only five or six months old. The clusters contain up to about fifty eggs, bound together by mucus, which hatch in about three weeks in the laboratory.

Ecology

In captivity, like most other slugs, *A. lusitanicus* is readily reared on lettuce, cabbage, oatmeal, etc.; but little is known of its habits in the wild.

Distribution (Map 9)

In the British Isles, known only from Berehaven, Bantry Bay, Ireland (Collinge, 1893); the garden of No. 24, North Bailey Road, Durham and the river bank adjoining (Quick, 1952); and the site of bombed cottages at Attleborough, Nuneaton, Warwickshire (Cain & Williamson, 1958). On the Continent, known from near Lisbon, Portugal; Mentone and Pyrenées Orientales, France; and Basle, Switzerland. The species may be indigenous to Ireland and but recently introduced to Durham and Nuneaton, though it seems firmly established there. Probably it is more widely distributed in Britain, but has not been distinguished from *A. ater*.

Material examined

Living specimens from Durham and Nuneaton. Spirit specimens from Basle, Switzerland, and the Pyrenées Orientales. An immatúre specimen from Bantry Bay (Collinge Collection, Museum of Zoology, Cambridge) probably belongs to this species.

Arion ater ater (Linnaeus, 1758)

Limax ater Linnaeus, 1758 : 652. Sweden.
Arion empiricorum Férussac, 1819 : 60, pls. 1–3 (in part).

First British record

By Lister (1674).

Diagnostic features

Large size, coarse tubercles, wide foot fringe, large respiratory orifice; short free oviduct surrounded by genital retractor muscle, ligula in upper atrium. Adults not certainly distinguishable in outward appearance from *A. a. rufus*, but usually black or dark brown with a grey sole, and rarely with a brightly-coloured foot fringe. Lateral pouch and ligula much smaller than in *A. a. rufus*, and vas deferens usually shorter. Upper atrium shorter than lower atrium.

External appearance (Pl. 1, fig. 3)

Length when fully extended generally about 14 cm, but may be even longer. The body tubercles are long and prominent, and darker than the furrows except in the young. The mantle is shagreened. There is no trace of a dorsal keel at any stage. The caudal mucus pore is conspicuous. The sole is more or less divided into median and lateral areas, the lateral areas usually the darker. The wide foot fringe is transversely lineolated, and in dark specimens the lines extend into the lateral areas of the sole. In pale individuals (except true albinos, which are rare) the head and tentacles are much darker than the rest of the body. The respiratory orifice is absolutely and relatively larger than in the previously described species. The very sticky body mucus may be colourless, or yellowish in red and yellow forms, that from the caudal pore always colourless. At rest, *A. ater*, like *A. lusitanicus*, but unlike *A. subfuscus* and the smaller species, can contract to a hemispherical shape, or even a larger portion of a sphere.

External variation

Since *A. a. rufus* has been generally considered as only a variety of *A. ater*, it is impossible at present to tell which of the very numerous named varieties belong properly to the latter. Probably most of the brighter varieties belong to *A. a. rufus*, and of the duller ones to *A. a. ater*.

Extensive lists of varieties are given by Taylor (1902–07), Kennard & Woodward (1926) and Hesse (1926), of which the following is a short selection: var. *ater* Linnaeus (1758), black with grey sole; var. *aterrima* Taylor (1905), completely black; var. *alba* Linnaeus (1758), white; var. *albida* Roebuck (1883), white with yellow fringe; var. *castanea* Dumont & Mortillet (1856), brown with paler fringe; var. *albolateralis* Roebuck (1883) (? = var. *media* Jensen, 1873), dorsum black, sides white; var. *reticulata* Roebuck (1885), tubercles pale, furrows pigmented (i.e. the juvenile colouring retained by the adult); var. *hiberna* Mabille (1868), rusty purple with paler sides; var. *plumbea* Roebuck (1884*a*), leaden grey with yellow fringe; var. *succinea* Müller (1774), yellow with red or orange fringe; var. *coccinea* Gistel (1848), vermilion; var. *marginella* Schrank (1803), black with red fringe.

Pallial organs

Large vessels occupy the roof and floor of the pulmonary chamber. The kidney is curved into a rounded quadrangular form, surrounding the pericardium, and the ventricle lies posteriorly to the auricle. The anterior branch of the aorta curves round the anterior loop of the intestine, then runs forwards supplying branches to the anterior part of the body, passing between the visceral and pedal ganglia. The posterior aorta runs backwards and supplies the alimentary and genital systems, and passes between the visceral and pedal ganglia. The ureter and rectum terminate at the posterior lip of the respiratory orifice.

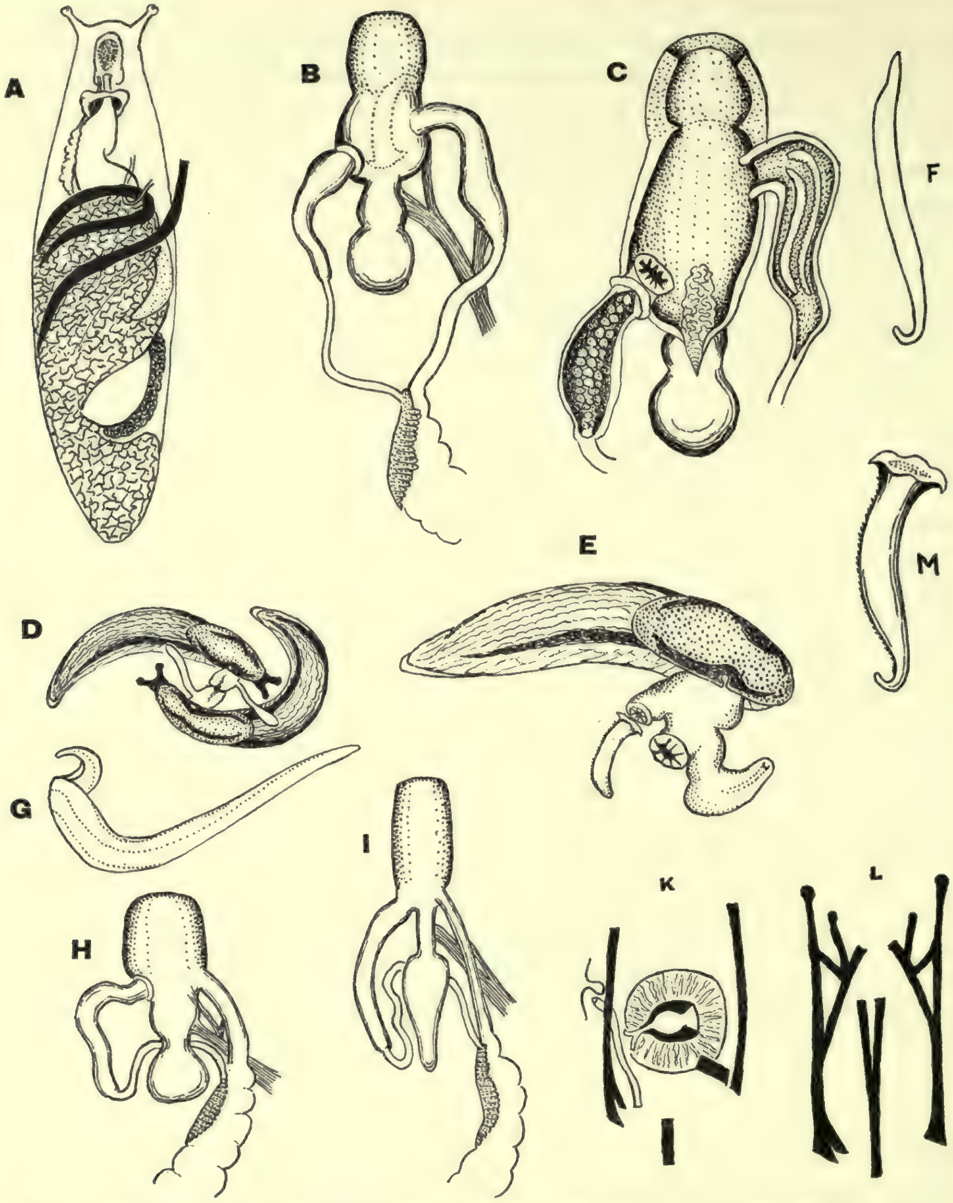

FIG. 4. *Arion.* **A.** *A. hortensis*—internal organs *in situ* (× 2) showing liver, exposed part of stomach, part of ovotestis, albumen gland, intestine, aorta, crop, left salivary gland, nerve ring, characteristic pigmented area on buccal bulb. **B.** *A. hortensis*—distal genital ducts (× 4) with position of the partner's spermatophore indicated on upper atrium. **C.** *A. hortensis*—distal portion of genital ducts (× 5·3) opened to show ligula in oviduct, glandular area below spermatheca, and papillate mucous membrane of epiphallus. **D.** *A. hortensis*—mating pair (× 1·3) with slender parts of oviducts everted and functioning as stimulators. **E.** *A. hortensis*—individual

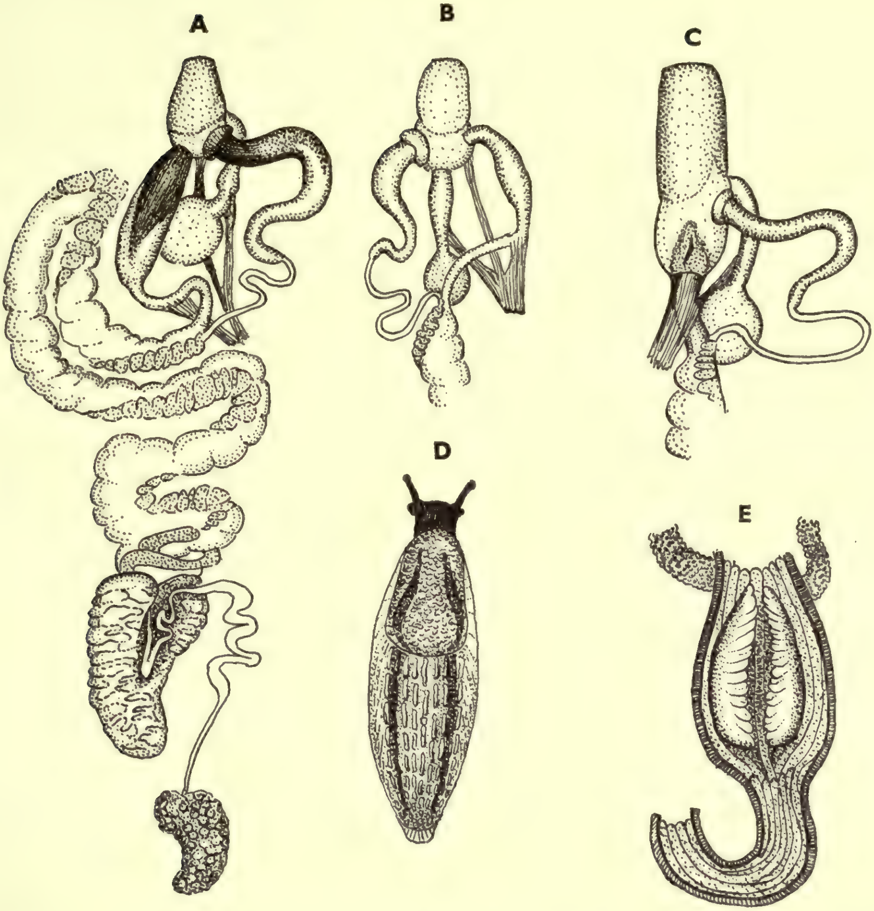

FIG. 5. *Arion.* **A.** *A. lusitanicus*—reproductive organs (× 3). **B.** *A. subfuscus* —distal genital ducts (× 3). **C.** *A. ater ater*—distal genital ducts (× 3). **D.** *A. lusitanicus*—young individual (× 10). Compare mantle bands with those of young *A. subfuscus* and *A. ater* (pl. 1, figs. 9 & 11). **E.** *A. lusitanicus*—oviduct (× 5·3) opened to show position of ligula.

immediately after coitus (× 2) with everted genitalia, showing atria, everted oviduct, papillate epiphallus, partner's spermatophore adhering to base of spermatheca duct. **F.** *A. hortensis*—spermatophore (× 6·7). **G.** *A. fasciatus*—spermatophore (× 4), adapted from Lohmander. **H.** *A. intermedius*—distal genital ducts (× 4·7). **I.** *A. fasciatus*—distal genital ducts (× 4). **K.** *A. hortensis*—pallial region in ventral view, showing kidney, pericardium, auricle, ventricle, rectum and respiratory orifice. Muscles cut short. **L.** *A. hortensis*—cephalic and buccal retractor muscles, ventral view. **M.** *A. ? hortensis*—spermatophore (× 6·7) of a slug from a garden in Eaton Crescent, Swansea, Glamorgan.

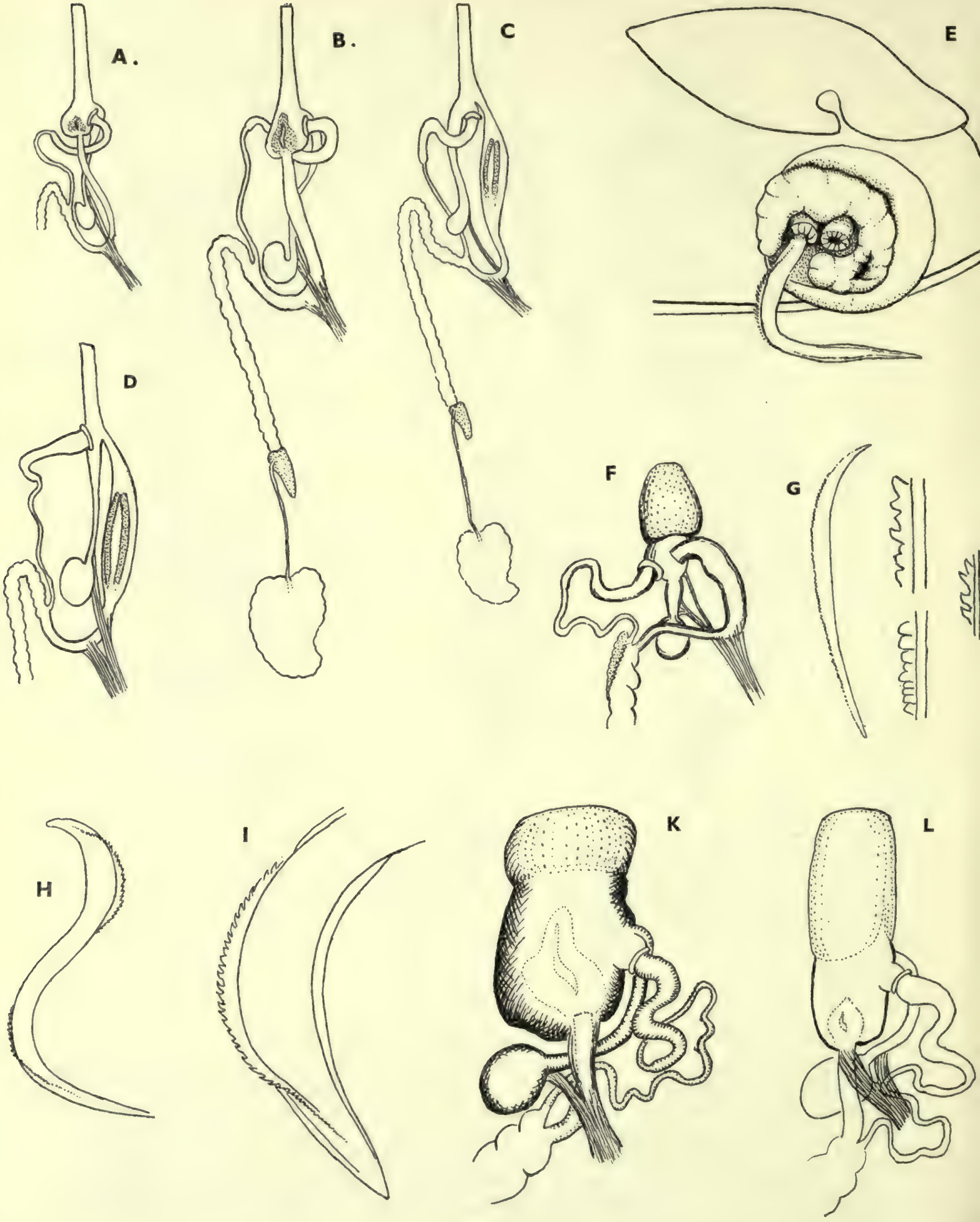
A.
B.
C
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FIG. 6.

Retractor muscles

The right and left cephalic retractors are widely separated at their origin, from the diaphragm behind the kidney. The pharyngeal retractor arises from the median dorsal body-wall. The genital retractor arises from the diaphragm immediately in front of the origin of the left cephalic retractor, ensheathes the short free oviduct, and sends a branch to the spermatheca duct.

Nervous system (see Text-fig. 7 M)

Highly concentrated in the adult, the commissures being short and the visceral ganglia closely united.

Jaw

Strong, arcuate, 3·5 mm across, crossed by a varying number of ribs (up to eighteen), variable in breadth, which denticulate the upper and lower edges. Colour yellow in pale specimens, nearly black in dark ones, the attached margin being darker than the free cutting edge.

Radula (Text-fig. 3 F)

7–8 mm long by 3 mm wide. The number of lateral teeth varies from 20 to 25, and of marginals from 40 to 46 on each side, but the average formula is C.22.44 × 130.

Alimentary system

The short oesophagus leads through a large wide crop to the stomach, which forms the posterior part of the alimentary canal. The salivary glands on each side of the crop are large, flattened and much lobulated. The intestine, with one anterior loop, is twisted through about one and a half turns—more than in the young of the smaller species.

Reproductive system (Text-figs. 5 C and 6 L)

The proximal parts resemble those of other species of *Arion* (see Text-fig. 5 A).

FIG. 6. *Arion.* **A.** *A. ater ater*—distal genital ducts (× 10) of a young individual, showing long atrium and position of ligula. **B.** *A. ater ater*—genital organs (× 3·3) of a nearly full-grown but immature individual, showing relative sizes of ovotestis, albumen gland, common duct and distal portions of ducts. **C.** *A. lusitanicus*—genital organs (× 6·7) of an immature individual, showing relative sizes of organs and position of ligula. **D.** *A. subfuscus*—distal genital ducts (× 6·7) of a young individual, showing ligula in lower oviduct. **E.** *A. lusitanicus*—slug after coitus, with atrium everted. The ligula, with the oviducal orifice in its lower anterior part, surrounds the orifices of epiphallus and spermatheca. The partner's spermatophore projects from the spermatheca duct. **F.** *A. subfuscus*—distal genital ducts (× 3·3). **G.** *A. subfuscus*—spermatophore (× 3·3), and portions of spermatophore (× 16·7) from near anterior end, centre and posterior end. **H.** *A. lusitanicus*—spermatophore (× 3·5). **I.** *A. lusitanicus*—portion of posterior end of spermatophore (× 11). **K.** *A. ater rufus*—distal genital ducts (× 3·3). **L.** *A. ater ater*—distal genital ducts (× 3·3).

The short free oviduct, ensheathed by the genital retractor, enters the upper atrium apically. It is not dilated, and does not contain the two conspicuous folds of *A. hortensis*, *A. subfuscus* and *A. lusitanicus*. However, the upper atrium contains a somewhat similar folded mass, arising from the walls of the atrium and the termination of the oviduct, known as the ligula. This is much smaller than in *A. a. rufus*, where it is contained in a lateral enlargement of the atrium. The spermatheca duct is relatively longer than in *A. intermedius*, *A. fasciatus*, *A. hortensis* and *A. subfuscus*, is not bulbous at the base, and receives a branch from the genital retractor. The vas deferens is usually less than one and a half times as long as the epiphallus, which terminates in a thickened ring at the atrium.

Spermatophore (see Text-fig. 7 L)

This rapidly disintegrates in the spermatheca, so that it can only be obtained intact soon after coitus. Two specimens were obtained in this way, which are 17 and 18 mm long. Each is somewhat dilated near the proximal end, and tapers in each direction. A finely serrated ridge runs nearly the whole length, the serrations pointing forwards. The epiphallus measures only 11 mm long in alcohol specimens ; so, unless it is much longer in life, part of the spermatophore must be formed during coitus.

Mating

Occurs in June and July, at any rate in Wales, after dark. After about half an hour of following and licking, the animals curve in a semicircle, neck to neck, and evert their atria to form a bluish-white mass. They separate after about half or three-quarters of an hour, when the spermatophores can be seen protruding from the spermatheca ducts, while the shrinking ligulae and atria are quickly withdrawn. Adams (1910), Gerhardt (1940) and Quick (1947) give fuller details.

Development

The eggs are variable in size, usually about 5 × 4 mm. They are opaque and leathery, pearly white when laid but turning brown. They are laid in clusters in the soil, two or three weeks after coitus. The first cluster may contain 150 eggs or more, and one or two subsequent clusters fewer than this. The eggs hatch in from four to six weeks. The young, 10 mm long, are pale straw colour or sometimes greenish, with darker head or tentacles. They are usually bandless, and if faint bands appear after a few days they quickly fade. Yellow pigment is concentrated in the tubercles. In the young of dark varieties the black pigmentation begins in the dorsal furrows and spreads downwards, producing a reticulate pattern which very occasionally persists in the adult ; though as a rule the pigment of pale adults is concentrated in the tubercles, leaving the furrows paler. The sole is the last part to pigment.

Like the other species of *Arion*, *A. ater* shows in the later stages of embryonic development a cephalic and a caudal vesicle, which pulsate alternately. The tubular caudal vesicle persists to within a few days of hatching (Text-fig. 18 F). The jaw at hatching does not show any sign of bilateral origin like that of *Agriolimax*.

Behaviour

Adults of *A. ater* exhibit a peculiar rolling reflex, if touched when fully (or almost fully) contracted. The body sways from side to side with a simultaneous screwing motion, with a periodicity of about two seconds. The movement cannot always be elicited, but may be quite violent. As far as is known, no other slugs show this reflex. It is tempting to explain it in terms of alternate contraction of the cephalic retractors, which have separated origins in *Arion*. However, the reflex is only doubtfully elicited from *A. lusitanicus*, and repeated attempts to elicit it from other British species of *Arion* have always failed.

Ecology

A. a. ater is practically omnivorous, eating decayed vegetable matter, dead mice and rabbits, and animal faeces. In the lowlands, it is common in grass fields, woods, hedgerows and waste ground, and on grassy downs and sea cliffs. It is often the only mollusc present on upland peaty moors and sphagnum bogs, where it is smaller than in the lowlands, and either black (often the var. *aterrima*) or very dark brown.

Distribution (Map 10)

The whole of the British Isles, northern and central Europe, Iceland and ? Russia. Probably some of the records from Spain, Portugal, Italy and the Mediterranean coasts and Atlantic isles refer to the related forms (*A. a. rufus*, *A. lusitanicus* and possibly others). Introduced into North America.

Material examined

Living specimens of *A. a. ater*, as distinct from *A. a. rufus*, have been identified from the following localities in the British Isles: Exeter, Littlehampton and Collompton in Devon; Netley Heath, Surrey; Howe Wood near Littlebury, Essex; Reading, Berkshire; Thorpe St. Andrews, Brundall Marshes and Wheatfen Broad in Norfolk; Little Shelford, Homingsea and Durnford Fen in Cambridgeshire; Cefn Bryn, Gower and Llangennith in Glamorgan; Capel-y-ffin, Brecon; Skokholm Island, Pembroke; Abersoch, Caernarvon; Bromborough, Cheshire; Pentland Hills, Edinburgh; Courtmacsherry, Cork.

Arion ater rufus (Linnaeus, 1758)

Limax rufus Linnaeus, 1758 : 65. ? Sweden.
Arion empiricorum Férussac, 1819 : 60 (in part).
Arion sulcatus Morelet, 1845 : 28.

Notes

See Quick (1947). Økland (1923) believes it to have been introduced to Sweden in historical times. Férussac's *empiricorum* includes *A. a. ater*, *A. a. rufus*, and perhaps also *A. lusitanicus* and other species. Moquin-Tandon's description (1855–56, **2** : 10) of *empiricorum*, and his fig. 1 on pl. 1, could serve for either *A. a. ater* or

A. a. rufus; but his fig. 12 represents the genitalia of *A. subfuscus, A. lusitanicus* or a similar species.

Cain & Williamson (1958) have studied pigmentation and genital anatomy in populations referable to *A. a. ater* and *A. a. rufus*. Their evidence suggests that only the former is indigenous to the British Isles, where *A. a. rufus* is an introduced alien associated with cultivated land. In Europe the natural ranges of the two forms seem not to overlap widely, since *A. a. ater* apparently occupies Scandinavia and *A. a. rufus* much of the rest of the continent, but it is not yet known how the two forms interact along their natural boundary. However, two populations near Oxford show the intermediacy of character combined with high variability which is to be expected from hybrids. This suggests that the two forms should be considered as geographical races.

First British record

By Gerhardt (1940), on specimens from Swansea, Glamorgan. The subspecies had been considered by previous British authors as merely a variety of *A. a. ater*.

Diagnostic features

Adult not certainly distinguishable from *A. a. ater* on external appearance, but usually yellow to reddish-brown, with a creamy yellow sole and bright orange or red foot fringe. Internally, upper atrium longer than lower, much larger ligula in lateral pouch, vas deferens usually longer than in *A. a. ater*. Young have mantle bands, rarely found in *A. a. ater*.

External appearance, external variation, pallial organs, retractor muscles, nervous system, jaw, radula, alimentary system

As in *A. a. ater*.

Reproductive system (Text-fig. 6 K)

As in *A. a. ater*, except for the distal genital ducts. The upper atrium is larger, and exhibits a lateral bulging that lodges a much larger ligula. The lower atrium is shorter than the upper. The vas deferens is relatively longer, usually more than one and a half times as long as the epiphallus and sometimes nearly twice as long. The oviduct, instead of entering the apex of the atrium formed by the lateral bulge, enters between this and the entrance of the epiphallus. Sometimes (as in specimens from Limeslade Bay, Swansea) the lateral bulge is narrower and prolonged further backwards. Occasional specimens of *A. a. ater* show a suggestion of a lateral bulge, but the size of the ligula, and the relative sizes of upper and lower atria and the vas deferens and epiphallus, serve to identify it.

Spermatophore (Text-fig. 7 L)

Probably longer than that of *A. a. ater* (about 25 mm long), and even more disproportionate to the size of the epiphallus in spirit material. This may be associated with the longer period of coitus, if the spermatophore is formed during coitus.

Mating

A. a. rufus attains maturity later in the year than *A. a. ater*, and mates in September and October, at any rate in South Wales. Mating resembles that of *A. a. ater*, except that coitus lasts for two hours. For further details, see Gerhardt (1940) and Quick (1947).

Development

The eggs are like those of *A. a. ater*. The newly-hatched young are pale yellow or orange, and differ from those of *A. a. ater* in having (at birth or after a few days) dark mantle and body bands, which persist for a few months. In individuals which will be dark when adult, the course of pigmentation is as in *A. a. ater*. The young can be distinguished from those of *A. subfuscus* by their coarser tubercles, and by the closer approximation anteriorly of their mantle bands (Pl. 1, figs. 9 and 11).

Behaviour

A. a. rufus shows the same rolling reflex as *A. a. ater*.

Ecology

In Britain, *A. a. rufus* is more likely to be found in gardens and parks (though sometimes at a considerable distance from dwellings) than in wilder places. It never seems to occur in peaty moors or sphagnum bogs ; though this may reflect its introduction by man, and consequent restriction to cultivated land, rather than dependence on calcium in the soil.

Distribution (Map 11)

Not fully known, since *A. a. rufus* has only recently been distinguished subspecifically from *A. ater*. Authentically known in Britain from Glamorgan, Somerset, Berkshire, Oxford, Essex, Cambridge and Leicestershire. It seems to be the native form in Europe south of Denmark, though the natural ranges of the two subspecies are insufficiently known.

Material examined

Living specimens from Monkton Coombe near Bath, Somerset ; Chingford, Essex ; Basildon, Berks ; Coombe End, Oxford ; Lords Meadow near Cambridge ; and the Swansea district, Glamorgan. Spirit material from Loughborough, Leicestershire ; Borgholm, Öland Island, Sweden ; Froedensborg, NE. Zealand, Denmark ; Canton Solothurn, Switzerland ; and from France, Corsica and Portugal.

Superfamily ZONITACEA

Family LIMACIDAE

Slugs with a small calcareous shell almost always completely enclosed by the mantle. The dorsum is keeled posteriorly or right up to the mantle. There is no caudal mucus gland. The sole is tripartite and a supra-pedal groove is present (aulocopod). The jaw is smooth, usually with a median projection (oxygnath), and the lateral radular teeth are tri- or bicuspid, the marginal teeth aculeate. The spermatheca duct is short, generally arising from the atrium.

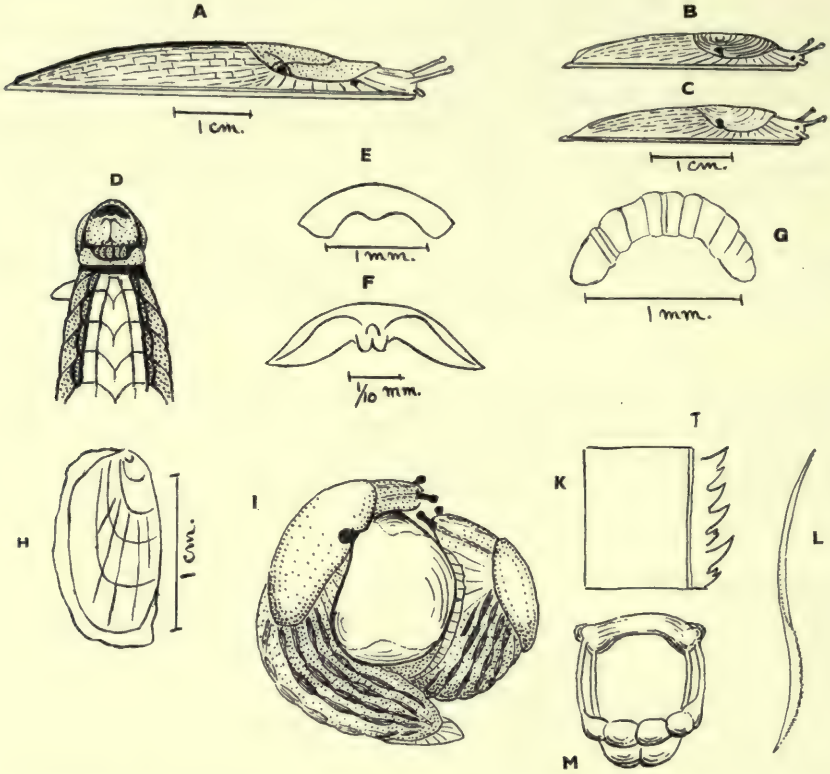

FIG. 7. Limacidae. External appearance. **A**. *Milax*—keel extending forward to mantle ; mantle granulate with horseshoe furrow ; respiratory orifice behind centre of mantle ; genital orifice between upper tentacle and respiratory orifice. **B**. *Agriolimax*—keel extending only a little way forward ; tail truncate ; mantle concentrically ridged with nucleus over respiratory orifice, behind centre of mantle ; genital orifice close behind upper tentacle. **C**. *Limax*—keel extending a little way forward ; tail not truncate ; mantle concentrically ridged with nucleus in median dorsal line ; respiratory orifice behind centre of mantle ; genital orifice close behind upper tentacle. **D**. *Milax*—chevroned foot-sole, stimulator protruded.

E. *Lehmannia marginata*—jaw. **F**. *Agriolimax reticulatus*—jaw of very young individual, showing bilateral origin. **G**. *Arion hortensis*—jaw, for comparison. **H**. *Limax maximus*—shell.

Arion ater rufus. **I**. Pair in copula. **K**. Portion of posterior end of spermatophore (× 24). **L**. Spermatophore (× 1·7). **M**. Ganglia and commissures of nerve ring (buccal ganglia omitted).

Subfamily PARMACELLINAE

The shell is paucispiral, not completely enclosed by the mantle (in *Parmacella*), or flat and enclosed (in *Milax*). The mantle is granular, bearing a horseshoe-shaped groove, and the respiratory orifice lies behind the middle of the right margin. The genital orifice is between the respiratory orifice and right upper tentacles. The dorsum is keeled up to the mantle. The central and lateral radular teeth are tricuspid. The intestine has one forwardly directed loop, and the rectum lacks diverticula. An epiphallus secretes a spermatophore, and atrial glands are present. *Milax* is the only British genus.

Watson (1930) considers that *Parmacella* and *Milax* arose from a common stock ; *Parmacella,* with its spiral shell, embedded pedal gland, and ocular retractor crossing the penis, being the more primitive.

Genus ***MILAX*** Gray, 1855

Type species *Limax gagates* Draparnaud, 1801.

The shell, completely enclosed by the mantle, has a median non-spiral nucleus near the posterior margin. The pedal mucus gland lies free in the body cavity, and not embedded in the foot below it, as in the other genera. The right ocular retractor lies to the left of both penis and vagina. In *M. sowerbyi* and *M. gagates* an atrial stimulator is present. The median area of the sole is crossed by ʌ-shaped grooves. *Milax* is without lateral body bands at all stages of growth.

Watson (1930) considers that, of the British species of *Milax, M. gagates* (with more lateral and fewer marginal radular teeth, and a wider distribution) is the most primitive, and *M. budapestensis* (with fewer lateral and more marginal teeth, and no stimulator) the most specialized.

A common continental species, *M. marginatus* (Draparnaud, 1801) (= *M. rusticus* Millet, 1843), which it seems possible may yet be discovered in Britain, is a yellowish slug with small black spots on the body and mantle and a dark band on each side of the latter, and resembles *M. budapestensis* in lacking the atrial stimulator.

Milax gagates (Draparnaud, 1801)

Limax gagates Draparnaud, 1801 : 100. Presumably near Montpellier, France.
Amalia parryi Collinge, 1895*a* : 7.
Amalia babori Collinge, 1897*c* : 294.

Notes

Two species are currently confused under the name *gagates.* The common British species is distinguished by its smooth genital stimulator, and less certainly by its smoother appearance (with flattened tubercles) and paler sole. The second species is primarily Mediterranean in distribution, though there is one hitherto unpublished

British record (p. 156). It has two rows of large papillae on the stimulator, and also more prominent tubercles and a darker sole.

It is not easy to determine the proper application of the name *gagates*. There are no slugs among Draparnaud's types at the Naturhistorisches Museum, Vienna (Locard, 1895 : 154 ; confirmed by Dr. O. E. Paget *in litt.*). Both species occur at Marseilles, only eighty miles from Draparnaud's home at Montpellier. Draparnaud's description does not deal with the internal anatomy. However, he describes *gagates* as " très-lisse, très-luisante " (1801) and " nitidus ; corpore striato subrugoso" (1805). This strongly suggests the north-western species, since he applies " subrugosus " to other slugs as smooth as this, and uses " rugosus " only for those as rough as the Mediterranean species.

Few early authors described or figured the condition of the stimulator, from which alone their application of the name *gagates* could be determined. Lessona & Pollonera (1884 : 105, pl. 2, fig. 2) use this name for Italian slugs with papillate stimulators. Germain (1930, fig. 52 A), in treating the French fauna, gives a figure of a papillate stimulator which is apparently copied from Lessona & Pollonera, and does not mention the locality. Taylor (1902–07, fig. 159) shows the smooth stimulator of a British slug.

The name *parryi* Collinge is a synonym of *gagates*, as the latter is here interpreted, since one of the type specimens from Santa Cruz, Teneriffe, shows on dissection a penis, epiphallus and stimulator like the British species. So does one of a series from Haleakala Maui, Hawaii, apparently the types of *babori* Collinge. The following names, among others, cannot at present be allocated to either of the species with any certainty :

Limax maurus Quoy & Gaimard, 1824 : 427. Port Jackson, Sydney, Australia.
Parmacella nigricans Schultz, 1836, **1** : 125. Palermo, Sicily.
Amalia mediterranea Cockerell, 1891 : 331. Algeria.
Amalia mediterranea forma *similis* Cockerell, 1891 : 332. Catania, Sicily.

However, specimens that I received from Catania in 1947 proved to be the species with a papillate stimulator.

First British record

By Thompson (1840 : 205).

Diagnostic features

Uniform grey or black colour, with darker keel, respiratory orifice without pale margin, mucus colourless ; smooth genital stimulator, rather thick spermatophore, not hooked at the thick end and with spines distributed more evenly than in *M. sowerbyi*.

Differs from *M.* cf. *insularis* in smooth, not papillate, stimulator ; and less certainly in smoother skin and paler sole.

External appearance (Pl. 1, fig. 12)

Length extended about 5 cm. When contracted, the slug is more compressed laterally than *M. sowerbyi*. The colour is usually grey or black, getting lighter towards the foot. The tubercles are flattened, making the slug rather smooth, and the intervening grooves are unpigmented. The keel is usually dark, and is abruptly angulated at the posterior end. The central area of the granulate mantle is delimited by a horseshoe-shaped groove, open posteriorly, with the arms angulated at the level of the respiratory orifice. The respiratory orifice is small and without a pale border, and is situated a little behind the centre of the right margin of the mantle. The sole is pale, distinctly tripartite, with the median zone crossed by Λ-shaped grooves (Text-fig. 7 D). Only this central area shows the locomotory waves. The mucus is sticky and colourless.

External variation

Var. *plumbea* Moquin-Tandon (1855), paler or darker grey; var. *rava* Williams (1888), drab coloured, slightly fuscous, mantle paler; var. *bicolor* Taylor (1904), deep red on the sides; var. *benoiti* Lessona & Pollonera (1882), black, keel whitish.

Other varieties with a Mediterranean distribution mentioned by Taylor (1902–07 : 143–146) probably refer to *M*. cf. *insularis*.

Shell (Text-fig. 8 K)

Measures about 4 × 2·5 mm. White and shining. Somewhat saddle-shaped above, and flattened below. The nucleus is near the posterior margin, in the middle line, and the lines of growth are distinct. Viewed laterally, the shell is concave from back to front, with the nucleus at the highest point, and shows a groove separating the upper part of the shell from the lower.

Pallial organs

The kidney has an extension to the right toward the rectum, and the auricle and ventricle lie anterior to the left half of the kidney. The rectum crosses over the common origin of the tentacular and pharyngeal muscles to the posterior lip of the respiratory orifice.

Pedal gland

Lies free in the body cavity, occupying half the body length. Its duct projects posteriorly from the glandular tissue for about 0·25 mm.

Retractor muscles

The pharyngeal and tentacular retractors are not separated, as in *Arion*, but have a common origin from the posterior edge of the diaphragm in the middle line. At the posterior border of the kidney this divides into the pharyngeal retractor, which is bifurcate for about one-third of its length, and the tentacular retractor. The latter soon divides into right and left branches, and these divide again much further forward into branches to the upper and lower tentacles. The penial retractor arises further forward, on the left side of the diaphragm.

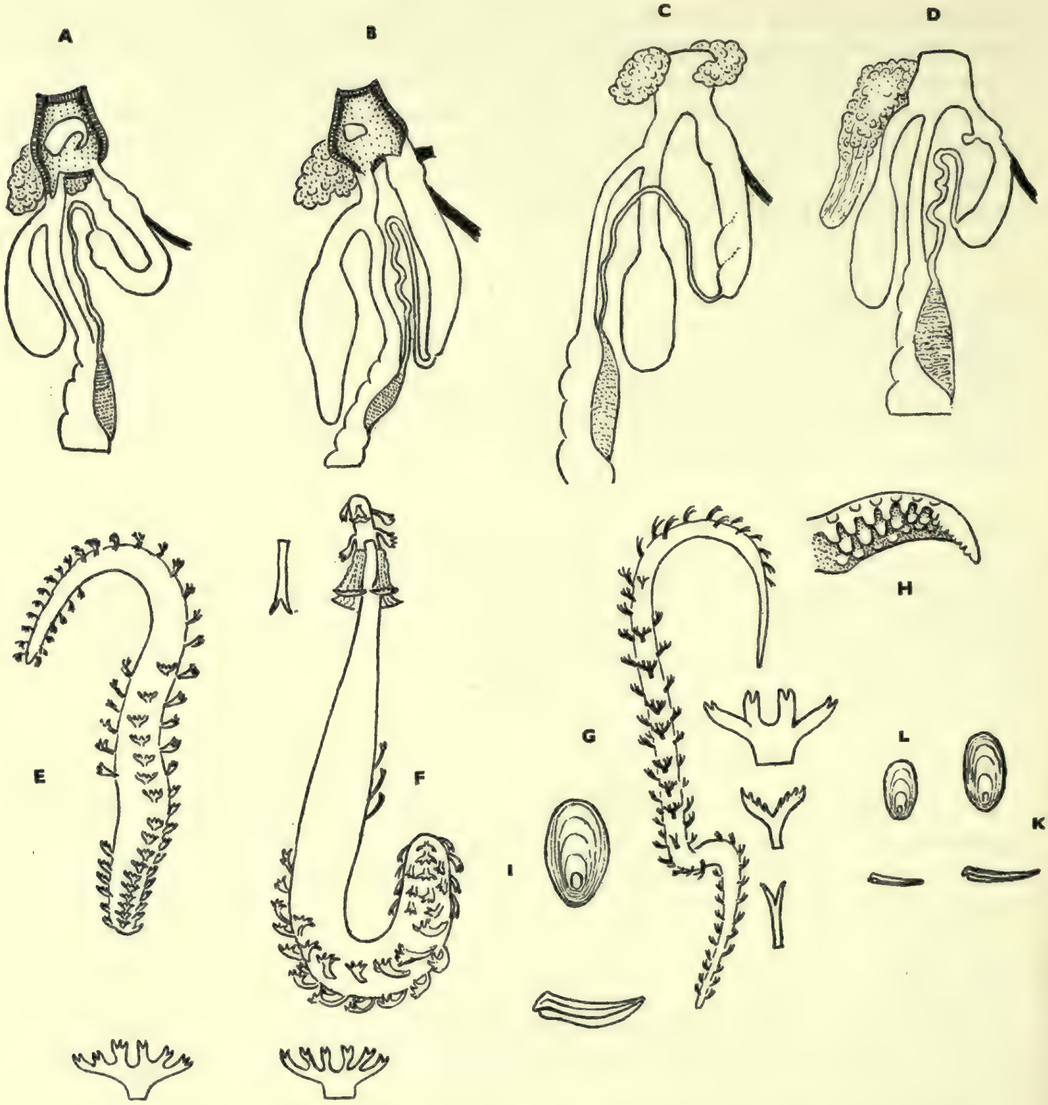

FIG. 8. *Milax*. Distal genital ducts (× 4). **A.** *M. gagates*—atrium opened to show stimulator. **B.** *M. sowerbyi*—atrium opened to show stimulator. **C.** *M. budapestensis*. **D.** *M.* cf. *insularis*.

Spermatophore (× 6·7), spines (× 33). **E.** *M. gagates*—one spine. **F.** *M. sowerbyi*—two spines. **G.** *M. budapestensis*—three spines.

H. *M.* cf. *insularis*—papillate stimulator.

Shell (× 2·7), dorsal and lateral views. **I.** *M. sowerbyi*. **K.** *M. gagates*. **L.** *M. budapestensis*.

Nervous system

The cerebral ganglia are connected by a short broad commissure. The cerebro-pleural and cerebro-pedal commissures are short, so that the nerve ring closely surrounds the oesophagus. The pleural, visceral and abdominal ganglia are closely approximated, as are also the visceral and pedal ganglia. The abdominal ganglion is almost completely fused with the left visceral. There is little if any variation in the nervous system between the species of *Milax*.

Jaw

Brown, oxygnathous, measuring 1·7 mm across.

Radula (Text-fig. 9 A)

The central tooth has a mesocone and well-developed ectocones. The laterals have well-marked endo- and ectocones, nearly equal in size. Most of the marginals lose the ectocones, but five or six of the innermost teeth retain them. Formula C.17.27, with slight variation (see p. 157).

Alimentary system

The brown oesophagus leads to a long capacious crop, and the intestine (which exhibits marked spiral torsion) extends well behind the stomach, thus contrasting strongly with the condition in *Arion*. The rectum runs forwards above the common stem of the retractor muscles.

Reproductive system (Text-fig. 8 A)

The spiral ovotestis, mainly hidden by the upper lobes of the liver, gives off the pale hermaphrodite duct. This is much folded in its anterior wider part, and the terminal slender portion bears an oval seminal vesicle at its entry into the linguiform albumen gland. The common duct is long, voluminous and folded. The spermatheca is an oval sac, with a short duct arising from the oviduct 1·5 mm before its termination.

The prostate is a yellow ribbon-like organ on the common duct. At the beginning of the free oviduct it gives off the somewhat convoluted vas deferens, which enters the apex of the epiphallus. The epiphallus is widest apically and has a rounded eminence or blunt caecum below the apex, a feature that is not shared by *M. sowerbyi* or *M. budapestensis*. At the insertion of the retractor muscle, the epiphallus, without any external sign, passes into the penis, which narrows towards its termination in the atrium. Before its termination the penis shows two more or less distinct dilatations, the upper one containing the blunt perforate penial papilla with a small pigmented diverticulum. The mucous membrane of the epiphallus is thrown into transverse circular folds, and that of the penis into longitudinal folds. A lobulated gland that can be unravelled into long glistening white tubules opens into the atrium. The atrium lodges a fleshy conical stimulator attached by its larger end, with the tip often folded back. The stimulator is generally smooth but occasionally has two or three minute papillae near the tip.

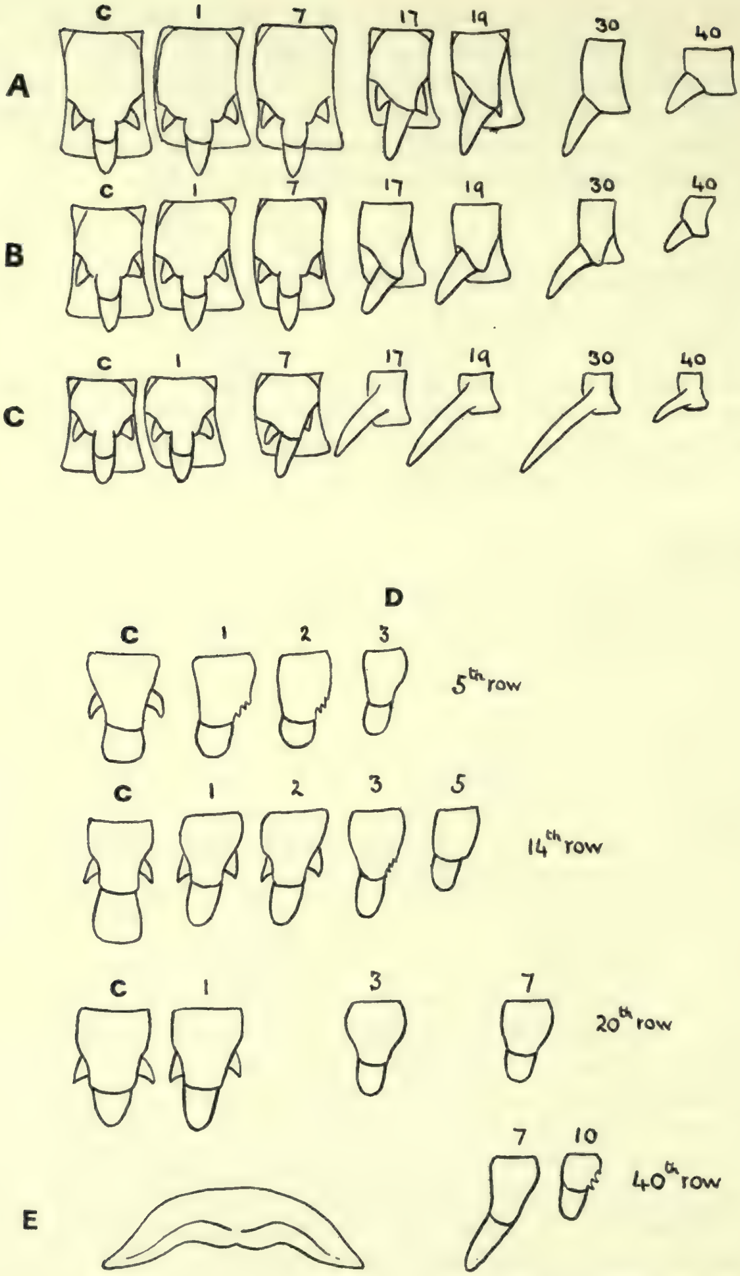
c 1 7 17 19 30 40
A
c 1 7 17 19 30 40
B
c 1 7 17 19 30 40
C
D
C 1 2 3
5th row
C 1 2 3 5
14th row
C 1 3 7
20th row
7 10
40th row
E

FIG. 9. Representative radular teeth (× 330). **A.** *M. gagates.* **B.** *M. sowerbyi.* **C.** *M. budapestensis.*

M. sowerbyi, an individual one day old. **D.** Representative radular teeth (× 1,000). **E.** Jaw (× 67).

Spermatophore (Text-fig. 8 E)

A brown chitinous tube about 10 mm long, widest at the centre and narrowing at the anterior end. Except at two places on the concave side, it bears prominent spines throughout. The spines have four main branches, and fourteen or sixteen terminal points.

Mating

Observations are very scanty, but apparently the partners during coitus are in close contact, and little or nothing of the genitalia is visible. Though the stimulator is often found protuded in spirit specimens, it is not visible during coitus. Mating has been recorded in spring, summer and winter. Taylor describes the eggs as 2 × 1·5 mm, transparent and thin shelled. This, if correct, is much smaller than the eggs of *M. sowerbyi* and *M. budapestensis.*

Ecology

Though widely distributed in the British Isles, *M. gagates* seems to be commoner near the sea than inland, and especially common in the south-west. In parts of Devon it is abundant in root crops, and can be a pest. It inhabits cliffs, wild places and gardens. In captivity, like most other slugs, it eats carrot, potato and oatmeal.

Distribution (Map 12)

M. gagates probably occurs in all the vice-counties of England, Wales and Ireland, the south of Scotland, the Isle of Man and the Clyde Islands. In Europe, its distribution is essentially north-western, though specimens from Marseilles have been examined. Other records from the Mediterranean area probably refer to a closely-related species, here distinguished as *M.* cf. *insularis* (p. 156).

M. gagates has been introduced into South Australia, Hawaii, California, Canary Isles and Tristan d'Acunha. It is not yet clear whether other records of introductions into America, Bermuda, Ascension Island, St. Helena, South Africa, Australia, Tasmania, New Zealand and Polynesia refer to *M. gagates* or to *M.* cf. *insularis.*

Fossil record

Pleistocene to Recent.

Material examined

Living specimens from Epsom, Surrey ; Southwell, Nottingham ; Porthcawl, Glamorgan ; Haverfordwest, Pembrokeshire ; St. Agnes, Scilly Isles ; and Majorca. Spirit specimens from Aberdeen, and from Marseilles, France ; Santa Cruz, Teneriffe ; Calbaden Canyon, Puenta Hills, Los Angeles, California ; Kensington suburb, Adelaide, South Australia (coll. B. C. Cotton) ; and Haleakala Maui, Hawaii.

Milax cf. **insularis** (Lessona & Pollonera, 1882)

Amalia insularis Lessona & Pollonera, 1882 : 57 (see 1884 : 103). Sardinia and Sicily.
Amalia ichnusae Lessona & Pollonera, 1882 : 60 (see 1884 : 106). Sardinia.

Notes

If the name *gagates* is to be reserved for the north-western species with the smooth stimulator (p. 149), the valid name for the present species remains to be determined. Several names whose application is uncertain (some of which are listed on p. 150) are available within the *gagates* complex. It will require a thorough study of the Mediterranean forms to clarify the biological and nomenclatural situation.

First British record

This is the first record to be published. Mr. Armitage collected specimens near Bexhill, Sussex, about 1948, and the differences between these and *M. gagates* were confirmed by Mr. Watson (*in litt.*). All other specimens examined, from various parts of Britain, have proved to be *M. gagates.*

Diagnostic features

Differs from *M. gagates* in having large papillae on the atrial stimulator. Also, the slug is usually larger, blacker and less smooth, with a darker sole.

External appearance

As *M. gagates,* except for the usually larger size, more prominent tubercles, and more intensely black coloration, with the sole not conspicuously paler.

External variation

It is not at present possible to assign named varieties to this poorly understood species.

Shell, pallial organs, pedal gland, retractor muscles, nervous system

As in *M. gagates,* as far as is known.

Jaw

As in *M. gagates,* though varying from pale brown to nearly black in the material examined.

Radula

The teeth closely resemble those of *M. gagates* in form and number. Formulae of radulae examined were : *M.* cf. *insularis* C.18.28 (Catania, Sicily), C.17.28 × 105 and C.19.27 (Malta), C.20.30 × 102 (Marseilles); *M. gagates* C.15.31 × 100 (Aberdeen), C.16.27 (Porthcawl), C.17.27 × 96 (California), C.19.27 × 102 (Marseilles).

Alimentary system

As in *M. gagates.*

Reproductive system (Text-fig. 8 D)

Here the differences from *M. gagates* are obvious. The stimulator (Text-fig. 8 H), instead of being smooth or having at the most two or three minute papillae near the tip, has large papillae disposed in four longitudinal rows near the base, diminishing to two rows and becoming smaller towards the apex. Sometimes the papillae are mucronate, and in one specimen they were found to be partly retracted. The atrial glands extend further backwards than in *M. gagates,* in a tongue-like prolongation.

The epiphallus does not possess the sub-apical bulge seen in *M. gagates.* The small internally-pigmented accessory penial papilla, instead of being enclosed in the penis sheath, bulges externally; but it seems likely that this character varies with the physiological state of the animal, in both species.

Whereas Mediterranean specimens examined had four rows of papillae towards the bases of their stimulators, Lessona & Pollonera (1884, pl. 2, figs. 1 and 2; 6 and 7) figure "*gagates*" and *insularis* with only two rows. They describe *ichnusae* as having a single row of papillae, though their figure shows the stimulator as smooth (1884: 106 and pl. 2, fig. 4). Possibly there is more than one species with a papillate stimulator in the Mediterranean region. Mr. Aten of Zaandam, Holland, reports (*in litt.*) finding *M. gagates* and *M.* cf. *insularis* in the Pyrenées Orientales, and that the latter when young has only a single row of papillae. This suggests that *M. ichnusae* may be an immature form.

Spermatophore, mating, development, behaviour, ecology

Not known.

Distribution

In Britain, once recorded from Bexhill, Sussex. In Europe, found in the Mediterranean region. Occurs together with *M. gagates* near Marseilles.

Fossil record

Not distinguishable from *M. gagates.*

Specimens examined

Spirit specimens from Marseilles and Valence, Malta, Sicily and Majorca.

Milax sowerbyi (Férussac, 1823)

Limax sowerbyi Férussac, 1823, **2** : 96, pl. 8. London.
Limax carinatus Risso, 1826 : 56.
Limax marginatus Jefferies, 1862 : 132.
Amalia maculata Collinge, 1895*b* : 336, pl. 23, fig. 6.
Amalia collingei Hesse, 1926 : 139.

First British record

By Férussac (1823).

Diagnostic features

Differs from *M. gagates* in brown colour speckled with darker patches, pale keel and margin of respiratory orifice, grooves between tubercles pigmented, keel not abruptly truncated, animal less compressed laterally when contracted, mucus yellow and more tenacious. Differs from *M. budapestensis* in broader, uniformly pale sole.

Internally characterized by short blunt atrial stimulator, long conical spermatheca, tapered spermatophore hooked at blunt end and bare of spines at narrow end.

External appearance (Pl. 2, fig. 23)

Length when extended about 7 cm. When contracted the slug is rather less compressed laterally than *M. gagates*, and the keel is not abruptly truncated behind. The body is usually pale or dark brown with darker speckling, with the keel paler and the grooves between the tubercles pigmented. The mantle grooves are as in *M. gagates*, but the respiratory orifice is pale margined. The tripartite sole is pale, and the sticky mucus yellow.

Variation

Var. *alba* Taylor (1904), entirely white; var. *fuscocarinata* Cockerell (1886*c*), keel the same colour as the back; var. *nigrescens* Cockerell, black with orange keel; var. *oretea* Lessona & Pollonera (1882), with median dark streak on mantle —found in Devon and Glamorgan.

Shell (Text-fig. 8 I)

Larger, thicker and more evenly oval than that of *M. gagates*, measuring 5 × 3 mm.

Pallial organs

As in *M. gagates*.

Pedal gland

The duct does not project beyond the glandular tissue.

Retractor muscles

The pharyngeal retractor is more deeply cleft than in *M. gagates*, and the two tentacular retractors separate sooner. The penial retractor arises nearer to the common stem of the other muscles, and there is a pair of short muscles from the penis to the body-wall.

Nervous system

As in *M. gagates*.

Jaw

As in *M. gagates*, but a little broader from upper to lower margin.

Radula (Text-fig. 9 B)

As in *M. gagates*, except that there are a few more transverse rows of teeth, and there are fewer laterals and more marginals in each row, with two or three of the innermost or transitional marginals often retaining a minute ectocone. Formula C.13.36 × 115.

Alimentary system

As in *M. gagates*.

Reproductive system (Text-fig. 8 B)

The lower genital ducts differ from those of *M. gagates* in several features. The short wide spermatheca duct arises from the free oviduct even nearer the atrium, and the sac has a narrowing backward prolongation. The epiphallus widens instead of narrowing towards its termination, and does not present the sub-apical lateral bulge of *M. gagates*, nor the small pigmented diverticulum at the distal end of the penis. The atrium contains a short blunt smooth stimulator.

Spermatophore (Text-fig. 8 F)

Thicker than in *M. gagates*, measures about 13 mm long. The thinner anterior end is smooth, and the curved posterior end bears recurved spines of three types. As usually found in the spermatheca, and figured by Taylor (1902–07, fig. 174) and others, the smooth anterior end terminates abruptly. However, if the spermatophore is taken very shortly after coitus, before the spermathecal fluid has had time to act upon it, the anterior end is found to be capped by a curious conical structure about 2 mm long, with a rounded apex, and formed by four leaflets with fringed edges (Quick, 1950). A fresh spermatophore of *M. budapestensis* does not have this cap, but no opportunity has occurred of examining a fresh spermatophore from *M. gagates*. Occasionally two spermatophores are found in the spermatheca in *M. sowerbyi*, but whether they are transferred during a single coitus (which is very prolonged) or on two separate occasions is not known.

Mating

After following and then curving around, the pair remain in close contact for twelve to eighteen hours, and little or nothing is visible of the genitalia. Pairing has been observed in October and November, but perhaps occurs at other times.

Development

The eggs are 4 × 3·5 mm, soft, translucent and pale amber, laid in clusters of about a dozen, hatching in from four to six weeks. The embryo before hatching has a large flattened caudal vesicle nearly circular in outline. When hatched the young are 8 mm long, with a conspicuous pale keel. The mantle is speckled with black and sometimes has a dark median streak, which is retained in var. *oretea* when adult.

Ecology

M. sowerbyi is found in gardens, cultivated fields and rubbish heaps. It burrows in the ground, and can do considerable damage to carrot and potato crops.

Distribution (Map 13)

Occurs in probably every vice-county of England, Wales, Ireland and the southern half of Scotland, and in France, Belgium and Spain. Probably known under other names from Portugal, Italy, Greece and the north coast of Africa. Introduced into South America and New Zealand?

Fossil record

Pleistocene to Recent.

Material examined

Living specimens from many places in Glamorgan, Pembroke, Surrey, Berkshire and Sussex. Spirit material from Britain and Marseilles.

Milax budapestensis (Hazay, 1881)

Limax gracilis Leydig, 1876 : 276, nec *Limax gracilis* Rafinesque-Schmaltz, 1820*a*.
Amalia budapestensis Hazay, 1881 : 40. Budapest.

First British record

By Phillips & Watson (1930).

Diagnostic features

Sole with dark central and paler lateral areas ; body when contracted tends to lie in a curve and is less compact and humped than *M. gagates* and *M. sowerbyi*. No atrial stimulator, spermatophore slender and spirally twisted. Radula has more marginal teeth, and spermathecal duct is longer, than in *M. gagates* and *M. sowerbyi*.

External appearance (Pl. 2, fig. 20)

The smallest British species of *Milax*, very slender when extended to 5 cm. The dorsum is dark, sometimes nearly black or with a brownish tinge, with a dirty yellow or orange keel. The grooves between the dorsal and the lateral, somewhat polygonal, tubercles are deeply pigmented. The mantle is sometimes paler than the dorsum, the horseshoe-shaped groove deeply pigmented, and the small respiratory orifice has a grey margin. The peripodial groove and margin of the sole are deeply pigmented, the lateral areas of the sole grey, and the median area dark grey or nearly black. The mucus is viscid and colourless, but in the mantle area becomes yellowish after repeated irritation.

External variation

Variation is confined to the intensity of the general grey colour ; to the tint of the keel, which varies from yellow to brownish-orange ; and to the sole, whose lateral areas are occasionally darker than the central area.

Shell (Text-fig. 8 L)

Concave or flat below, measuring 3 × 1·25 mm, brownish in colour.

Pallial organs

As in *M. gagates*.

Pedal gland

The duct extends behind the glandular tissue for about 5 mm.

Retractor muscles

The tentacular and pharyngeal retractors are usually rather more deeply cleft than in *M. gagates*, less so than in *M. sowerbyi*.

Nervous system

As in *M. gagates*.

Jaw

Brown and oxygnathous as in the other species but smaller, measuring about 1·5 mm across and 0·5 mm in height.

Radula

Differs from those of the other species in having the basal plate of the central tooth relatively broader, the aculeate mesocones of the marginals more slender, fewer lateral teeth and more marginals. Formula C.7–8.38–40.

Alimentary system

As in *M. gagates*.

Reproductive system (Text-fig. 8 C)

The pale spirally twisted ovotestis has five or six closely approximated lobes, each composed of numerous follicles. The hermaphrodite duct is slender for the greater part of its length, but becomes dilated and folded near the albumen gland, and here shows a small seminal vesicle. The common duct with a broad yellow prostatic ribbon is folded S-wise, and after parting from the vas deferens contracts to form a relatively long slender free oviduct. At about two-thirds of its length, the wider relatively long spermatheca duct arises, leading to a cylindrical sac with a rounded apex. The rather long flexuous vas deferens enters the epiphallus subapically. In the writer's experience the epiphallus and penis are long and slender, but Phillips & Watson (1930) describe and figure a short blunt form in addition, and find this the commoner. It is not known if this is a true dimorphism, or only the result of the physiological condition. Hazay (1881, pl. 1) shows an intermediate form of penis and epiphallus, and Simroth (1885, pl. 10, fig. 13) the long form. Both forms occur in Belgian specimens, sent to me by Dr. W. Adam. The atrium receives the slender ducts of a pair of lobulated atrial glands, and has no stimulator.

Spermatophore (Text-fig. 8 G)

Length about 16 mm, anterior end slender, posterior end spirally twisted. No trace of a frilled cap as in *M. sowerbyi*, even in spermatophores removed during or immediately after coitus. Except for the first 2 mm at the anterior end, the spermatophore is covered by forwardly-recurved branching spines, which are smaller and less branched towards the ends. There are two rows of spines anteriorly, three or four rows on the posterior two-thirds.

Mating

Occurs during November, December and January, under cover of loose stones or logs. Coitus generally starts in the evening and continues until the following mid-day or later. A little of the partly everted atria and the two penes is visible between the necks of the partners. The atrial glands are partly contained in the everted atria, together with the distal ends of the genital ducts.

Development

The ellipsoidal yellow leathery eggs are laid in small clusters underground, and measure 2·9 × 2·25 mm. Those laid in December hatch in March. The young at hatching are 4·5 mm long, pale yellowish-grey with a recognizable keel.

Behaviour

Whereas when at rest the other species of *Milax* assume a compressed helmet shape, *M. budapestensis* is usually found only half contracted, and curved into a semicircle.

Ecology

Occurs mostly in gardens and allotments, under stones and rubbish, and can do considerable damage to roots and tubers. Though much less common in wild places, there are records for such situations in Wales and Cheshire.

Distribution (Map 14)

Recorded from many localities in the British Isles, mainly in western England and Wales, but also in south-eastern England, southern Ireland and the Hebrides. On the Continent, known from Belgium, Germany (Würtemberg, Tübingen, the Rhön Mountains and Würzburg), North Italy (Verona, Vicenza and Padua), Hungary (Budapest), Transylvania, Bulgaria and Crimea. It probably occurs in many places between these widely-separated localities, in the zone from the British Isles to the Crimea. For a map and further details, see Phillips & Watson (1930) and Ellis (1951).

Fossil record

Recent.

Material examined

Living specimens from Berkshire, Glamorgan, Pembroke and Denbighshire. Spirit material from Britain and Belgium.

Subfamily LIMACINAE

Limacidae in which the keel rarely extends forwards as far as the mantle. The nucleus of the enclosed shell is terminal and lies to the left of the mid-line. The mantle is concentrically ridged and lacks a horseshoe-shaped furrow. There is no well-developed epiphallus, no spermatophore and no atrial gland. The stimulatory organ, when present, is a penial sarcobelum, and not an atrial stimulator as in *Milax*. The endocones of the lateral radular teeth, when present, are more or less united with the mesocones. The intestine has one or two forwardly-directed loops.

Genus ***AGRIOLIMAX*** Mörch, 1865

Type species *Limax agrestis* Linnaeus, 1758.

The right ocular retractor lies to the left of both penis and vagina. The intestine has one forwardly-directed loop, and the right lobe of the liver forms the apex of the visceral mass. A penial sarcobelum is present, more or less developed. The nucleus of the concentric mantle ridges lies to the right of the middle line, over the respiratory orifice. The tail is obliquely truncate.

Pilsbry (1944, 1948) adopts the name *Deroceras* Rafinesque-Schmaltz (1820*a* : 10) for this genus, as do most American and many European authors. Watson (1943 : 54) discusses the question. Ellis (in press) has submitted to the International Commission on Zoological Nomenclature a proposal for the suppression of *Deroceras* and other older names, and the validation of *Agriolimax*.

Hesse (1926) mentions sectional names for the first three species considered here. *Agriolimax* s.s. (including *A. agrestis* and *A. reticulatus*) has a rectal caecum and a more or less tufted penial appendix, whereas *Hydrolimax* Malm (including *A. laevis*) lacks both caecum and appendix, but has a long tubular penial diverticulum. Other sectional names have been proposed for groups of extra-limital species, such as *Krynickillus* Kaleniczenco, which lacks caecum, appendix and sarcobelum. However, several species show combinations of characters not covered by existing sectional names. *A. caruanae* has a tufted penial appendix like *Agriolimax* s.s., but lacks a rectal caecum like *Hydrolimax* ; while one or both of its penial diverticula may correspond to the latter's single but minutely bifid diverticulum. A slug collected in Cyprus by A. R. Waterston (? *A. cyprius* Simroth, 1906, or *A. panormitanus* Lessona & Pollonera, 1882) has a tufted appendix and a single diverticulum. Of two Abyssinian slugs described by Quick (1954), *A. gughensis* lacks caecum, appendix and diverticula but has a long, narrow, backwardly-directed sarcobelum ; while *A. scotti* lacks caecum, appendix and sarcobelum, but has two diverticula. In view of the intergradation and overlapping between species of which the anatomy is known, and of the number of species (especially in south-eastern Europe) of which it is not known, the use of sectional names within this genus does not seem useful.

Agriolimax reticulatus (Müller, 1774)

Limax reticulatus Müller, 1774 : 10. Denmark.
Limax canariensis d'Orbigny, 1839 : 47.
Krynickillus minutus Kalenickzenko, 1851 : 224.

Notes

The name *agrestis* has been used for this species by most British authors (see p. 170).

First British record

By Lister (1674 : 99).

Diagnostic features

Distinguished from *A. laevis* and *A. caruanae* by larger size, opaque appearance with very variable coloration, white sticky mucus and less active movements ; and internally by the presence of a rectal caecum. Differs from *A. agrestis* in the trifid crenulate penial appendix, and the posterior situation of the ovotestis.

External appearance (Pl. 2, fig. 15)

Length about 3·5 cm. The tail is obliquely truncated, the back keeled for a short distance at the hind end, and the sole tripartite. The respiratory orifice is at about two-thirds of the distance from front to back of the mantle, and the reproductive orifice close behind and below the right upper tentacle. The concentric striae of the mantle disappear in alcohol. The mucus is whitish on account of calcareous granules.

The colour is variable, with the body usually marked with brown or grey. The respiratory orifice has a conspicuous pale border.

External variation

The colour varies from pale cream to bluish-black, but is usually some shade of brownish-yellow, with darker grooves and scattered dark brown markings of varied shapes and sizes. Named varieties and subvarieties are very numerous. Many are practically synonymous, while some of those listed by Taylor (1902–07) refer to other species. Individuals often become darker as winter approaches. The following varieties may be recognized: var. *cineracea* Moquin-Tandon (1855), entirely ash coloured; var. *violacea* Gassies (1849), lilac or slate-coloured; var. *rufescens* Dumont & Mortillet (1856), rufous; var. *reticulata* Müller (1774), grooves dark, giving a reticulate appearance; var. *nigra* Morelet (1845), black, with pigment sometimes invading the sole. Albino forms occur occasionally.

Shell (Text-fig. 10 F)

The right border is convex.

Pallial organs (Text-fig. 10 A)

When the mantle is reflected to the right, a lobe of the kidney is seen to cover the rectum, and the short retractor penis to arise from the diaphragm at the anterior border of the pericardium.

Retractor muscles (Text-figs. 11 G and H)

The cephalic retractor muscles arise as a single stem in the mid-line, a short distance behind the diaphragm. The main stem usually divides basally, to form the right ocular retractor, and a common stem for the left ocular and the buccal bulb retractors (Text-fig. 11 G), but variations occur (Text-fig. 11 H). The genital retractor arises from the diaphragm near the front of the kidney, and is inserted between the vas deferens and the constriction above the sarcobelum.

Nervous system

This is very similar to that of *Milax.*

Jaw

Pale golden, of the usual oxygnathous type.

Radula (Text-figs. 11 L and O)

As in all *Agriolimax,* the endocones of the lateral teeth are delicate, lying close to the mesocone and on a slightly more superficial plane. The basal plates of the central and lateral teeth are larger and relatively narrower than those of *A. agrestis.*

Table I compares the radulae of the four British species of *Agriolimax.*

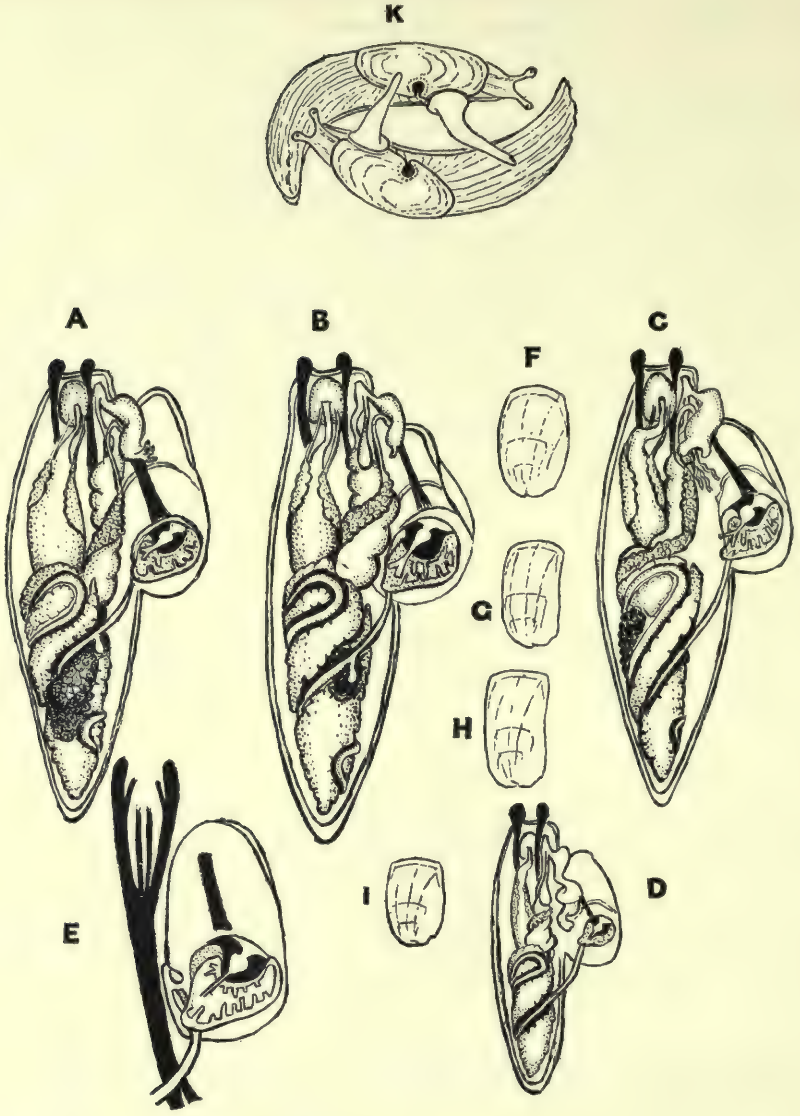

FIG. 10. *Agriolimax.* Dissection with mantle reflected to the right. **A.** *A. reticulatus*—(× 2), ovotestis extends much further backwards than in *A. agrestis.* **B.** *A. agrestis*—(× 2), ovotestis does not extend much further back than the rectal caecum. **C.** *A. caruanae*—(× 2·7), ovotestis far forwards, exposed on left side. No rectal caecum. **D.** *A. laevis*—(× 2·7).

A. caruanae. E. Pallial region and cephalic retractors (× 12). **K.** Mating pair with sarcobela protruded.

Shell (× 4). **F.** *A. reticulatus.* **G.** *A. agrestis.* **H.** *A. caruanae.* **I.** *A. laevis.*

TABLE I.—*Radular Formulae of the British Species of* Agriolimax *Mörch*

Locality	Date	Formula	Central tooth (mm)	Remarks
		Agriolimax reticulatus (Müller)		
Capel-y-ffin, Brecknock	20.vii.46	C.14.22 × 86	0·043 × 0·022	—
	20.vii.46	C.17.27 × 107	?	—
Blackpill, Swansea	17.viii.46	C.14.22 × 88	?	Small but mature.
Mumbles Rd., Swansea	23.viii.46	C.14.21 × 100	0·035 × 0·017	—
Porteynon, Glamorgan	? .xi.31	C.16.22	0·049 × 0·024	—
Clyne Valley, Swansea	7.ix.46	C.17.26 × 100	0·043 × 0·022	—
Llanwrtyd Wells	18.xi.38	C.6.8	—	Young, 8 mm long.
Burpham, Surrey	29.xii.46	C.18.26 × 122	0·052 × 0·026	—
		Agriolimax agrestis (Linnaeus)		
Wheatfen Broad	17.viii.46	C.16.23	0·038 × 0·019	Radula 3·2 × 1·7 mm.
	23.viii.46	C.16.23 × 105	0·040 × 0·02	—
	17.viii.46	C.14.21 × 100	0·034 × 0·017	—
	? .x.46	C.15.24	0·038 × 0·019	—
	? .ix.46	C.15.?	0·035 × 0·017	—
	?	C.15.21 × 100	0·032 × 0·016	—
		Agriolimax laevis (Müller)		
Singleton, Swansea	10.iii.48	C.13.27 × 92	0·023 × 0·012	Euphallic.
	2.viii.48	C.13.25 × 95	0·023 × 0·012	Hemiphallic.
		Agriolimax caruanae Pollonera		
Sketty, Swansea	? .x.31	C.14.50	—	—
	? .iv.32	C.14.55	—	—
Singleton, Swansea	31.i.35	C.10.?	0·023 × 0·014	Young, 12 mm.
Porteynon, Glamorgan	? .vii.46	C.14.55 × 118	0·029 × 0·017	Radula 3·1 × 1·5 mm.

Alimentary system (Text-fig. 10 A)

The lobulated salivary glands lie on each side of the crop, which narrows as it enters the small stomach. The posterior loop of the intestine extends behind the stomach towards the apex of the visceral mass, which is formed by the right lobe of the liver. The rectum has a small caecum overlying the ovotestis.

Reproductive system (Text-fig. 11 C)

The brown lobulated ovotestis lies towards the rear of the visceral mass, and is partly exposed on the surface (Text-fig. 10 A). The hermaphrodite duct is short and only slightly sinuous, with a seminal vesicle at its slender termination where it enters the albumen gland. The latter is short, shaped like a mammalian liver, and

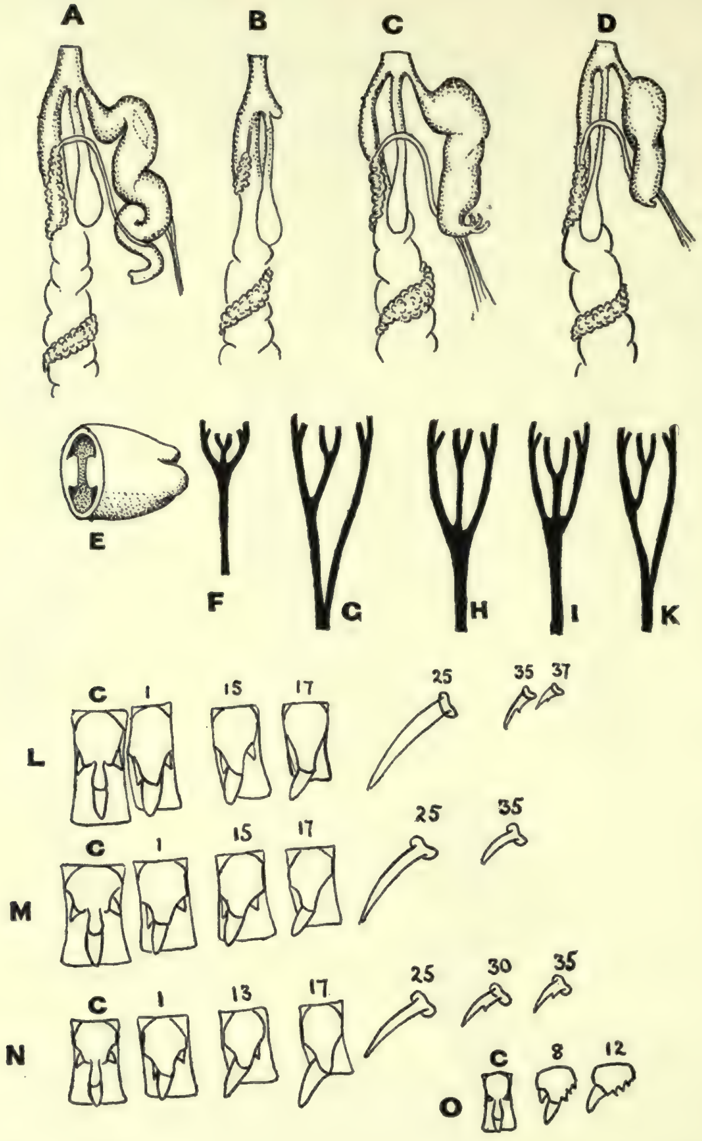
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FIG. 11. *Agriolimax*. Distal genital ducts (× 5·3). **A.** *A. laevis*—euphallic individual. **B.** *A. laevis*—aphallic individual. **C.** *A. reticulatus*. **D.** *A. agrestis*.

E. *A. laevis*—apex of penial appendage, showing bifid tip and two pilasters.

Cephalic retractor muscles. **F.** *A. laevis*. **G & H.** *A. reticulatus*. **I & K.** *A. agrestis*.

Representative radular teeth. **L.** *A. reticulatus*—(× 330). **M.** *A. agrestis*—(× 330). **N.** *A. laevis*—(× 330). **O.** *A. reticulatus*—(× 500) from young animal 8 mm long.

pale brown in colour. The common duct, with the lobulated prostatic ribbon, is thrown into zig-zag folds. The free oviduct is short and straight, and the atrium small. The spermatheca duct arises from the atrium and expands to a narrow oval sac. The short vas deferens enters the penis beyond its apex, beneath the genital retractor muscle. The penis is narrow basally, expands to a segment containing the triangular sarcobelum, and narrows a little before the apical segment. The latter terminates in a large penial appendage which is trifid, each branch having a crenulated outline. The details of the branching vary to some extent. The branches, which are tubular, are everted and turned completely inside out during mating, as in *A. agrestis* and *A. caruanae* (see Text-figs. 12 D and E).

Mating

This can occur throughout the year in Britain, even in the winter months, taking place on the surface usually after dark. The pair follow one another for from half to one hour in a narrowing circle, with copious exudation of mucus. The sarcobelum is protruded and plays over the partner's body. Then the animals remain still, neck to neck with bodies curved, and each atrium and penis is everted, bringing the oviduct and spermatheca duct to the surface. Then the base of the penial appendix appears and is explosively turned inside out, the branches appearing as long thin hyaline threads. A mass of sperms enclosed in a ball of mucus is simultaneously transferred from one partner to the other's everted mass, to which it adheres. The animals separate at once, and in a few seconds the genital complexes are invaginated and withdrawn, carrying the sperm packets with them.

Development

The eggs, laid about ten days after mating, are about 3 × 2·5 mm, translucent and speckled with calcareous dots which become absorbed during development. They hatch in two or three weeks, the young being 4 mm long, pale grey and translucent, and like all the British species have no bands at any stage. The young grow rapidly, and in warm weather may mature in three months. During late embryonic development the caudal and cephalic vesicles can be seen pulsating through the translucent shell, when the eggs are viewed under water (see Text-fig. 18 G). In Britain several broods are produced by a pair, and 700 eggs may be produced in a season. Luther (1915) states that self-fertilization occurs in *A. reticulatus* isolated from birth.

Ecology

A. reticulatus is perhaps the commonest British slug. It prefers drier sites than *A. agrestis* and occurs in grass fields, root crops, hedges, gardens and rubbish heaps, and under stones and logs in woods and coppices. It is often a serious pest in gardens and allotments, devouring seedlings and green crops.

Distribution (Map 15)

Ubiquitous in the British Isles. Probably indigenous to most of Europe, the

Mediterranean region and the Atlantic isles, and introduced by commerce into most parts of the world.

Fossil record

Pleistocene to Recent.

Material examined

Living specimens from many places in England and Wales. Spirit material from Britain, Europe, Atlantic isles, Réunion, America and New Zealand.

Agriolimax agrestis (Linnaeus, 1758)

Limax agrestis Linnaeus, 1758 : 652. Sweden.
Limax bilobatus Férussac, 1819 : 74.
Limax pallidus Schrenk, 1848 : 143.

Notes

The commonest British slug, *A. reticulatus* (Müller), was formerly regarded by British authors as a variety of *A. agrestis*, though Luther (1915) had shown them to be distinct. It is uncertain which of many synonyms in this group of slugs belong to *A. agrestis* and which to *A. reticulatus*.

First British record

By Ellis (1941). The slug was found at Wheatfen Broad, Norfolk, and determined by H. Watson.

Diagnostic features

Agrees externally with *A. reticulatus*, except that it is smaller, smoother and more slender and seldom has more than a few small dark flecks. Internally, the ovotestis lies further forward, and the penial appendix is short, smooth and unbranched.

External appearance

Like *A. reticulatus*, but rather slimmer and smoother, and less pigmented. The body is pale greyish-yellow, paler on the sides, sometimes with whitish calcareous-looking spots.

External variation

Occasionally, a few dark flecks are present and the grooves are slightly pigmented.

Shell (Text-fig. 10 G)

About 3 mm long, usually with the right border slightly concave.

Pallial organs (Text-fig. 10 B), *retractor muscles* (Text-figs. 11 I and K), *nervous system, jaw*

As in *A. reticulatus.*

Radula (Text-fig. 11 M)

The teeth are a little smaller than in *A. reticulatus*, and the basal plate wider (Table I, p. 167).

Alimentary system (Text-fig. 10 B)

As in *A. reticulatus.*

Reproductive system (Text-fig. 11 D)

The ovotestis lies further forward than in *A. reticulatus*, near the centre of the visceral mass, and is only partly exposed on the right side beneath the rectal caecum (Text-fig. 10 B). The remainder of the reproductive system is like that of *A. reticulatus*, except for the apex of the penis, which terminates in a single small curved digitiform appendix.

Mating

As in *A. reticulatus*. Mating occurs in Britain in the autumn, and perhaps at other times. Luther (1915) states that this species is incapable of self-fertilization, unlike *A. reticulatus.*

Development

The eggs are laid in clusters of from ten to twenty or more. They measure from 2·2 × 2·0 to 2·5 × 2·25 mm, and are more translucent and more finely dotted with calcareous particles than those of *A. reticulatus*. The newly hatched young are 3·5 mm long, translucent and whitish, and have no bands at any stage.

In Britain, the eggs are laid in the autumn and hatch in three or four weeks. The young mature in the following summer and autumn, and die in the late autumn after mating. In Finland, the life cycle is different (Luther, 1915), in relation to the more severe climate. The eggs are laid, and the parents die, in late August or September, while the eggs do not hatch until the following June. Thus embryonic life lasts for more than eight months in Finland and less than a month in England, while post-embryonic life lasts about three and twelve months respectively.

Ecology

In Britain, apparently confined to marshy carr (see Ellis, 1941) in East Anglia.

Distribution (Map 16)

In Britain, certainly recorded only from marshes by the Norfolk Broads : a single record of an immature specimen from North Uist (Ellis, 1951 : 196) has not been confirmed. Probably widespread in Europe, northwards to Finmark and Iceland, though the detailed distribution is uncertain because of confusion between this species and *A. reticulatus*. For example, Germain (1930) describes and figures *A. reticulatus* under the name *agrestis*.

Material examined

Living specimens from Wheatfen Broad, Sutton Broad and Alderfen Broad, all in east Norfolk.

Agriolimax laevis (Müller, 1774)

Limax laevis Müller, 1774 : 1. Frederiksdal, Denmark.
Limax brunneus Draparnaud, 1801 : 104.
Limax campestris Binney, 1844 : 52.
Limax hyperboreus Westerlund, 1876 : 97.
Agriolimax bevenoti Collinge, 1897*c* : 295.

Notes

Müller described his slug as " totum nigrum ", except for the median area of the sole, and compared its general appearance with that of the black land planarian *Rhynchodemus terrestris*. However, topotypes from Frederiksdal agree with the common slug, known as *A. laevis* in Britain, Europe and North America, in being some shade of brown. The discrepancy in colour is not highly significant, since the present species becomes very dark when somewhat dry and contracted, and since in America it varies in colour from amber to black (Pilsbry, 1948 : 540, 548 ; Altena, 1958 : 30).

Simroth (1885 : 222, pl. 9) described and figured, as forms of *A. laevis* from Germany, what are evidently representatives of two distinct species : those corresponding to the euphallic and aphallic forms of the widespread slug (his figs. 21 G and 22 H), and a larger and darker species with a hammer-headed penis (his figs. 17 C and 18 D). The latter is found principally in Germany and Poland, though it appears to have been introduced to Gotland Island, Sweden (Lohmander, *in litt.*). It has never been recorded from Denmark and Lohmander, despite his considerable experience of Danish slugs, has never found it there. Taylor's figures (1902–07, figs. 131 and 132), purporting to show the genitalia of British *A. laevis*, are copied from Simroth and show this second species.

It seems that the name *laevis* can properly be retained for the species to which it has long been applied. There is no reason to transfer it to the species with the hammer-headed penis, the correct name for which is uncertain.

First British record

By Johnston (1838 : 154), as *Limax brunneus*.

Diagnostic features

Small size, colour light or dark brown, smooth, active. Much smaller than *A. caruanae*. Head and neck extend further from the mantle than in *A. reticulatus*. Internally distinguished from the other species by its more sinuous penis, with a tubular caecum or appendix, and the frequent occurrence of aphallic specimens; and from *A. reticulatus* and *A. agrestis* by the absence of a rectal caecum.

External appearance (Pl. 2, fig. 19)

Length 1·7–2·25 cm. Light or dark brown, translucent, sometimes greenish, more or less flecked with darker spots. The respiratory orifice is less conspicuously pale-bordered than in the other species. The head and neck are thrust further forward than in *A. reticulatus* and *A. agrestis*, so that the mantle is more centrally placed, and the mantle has fewer concentric ridges. The mucus is clear, not milky. The slug is very active, and crawls rapidly.

External variation

The ground colour varies from pale to dark brown, with more or less darker flecking on body and mantle. Pale and dark specimens occur together at all seasons. Named varieties are var. *lacustris* Bonelli (in Lessona & Pollonera, 1882) (= var. *maculata* Cockerell, 1886*b*), irregularly spotted with dark brown; var. *grisea* Taylor (1904), grey or greenish-grey.

There is also marked genital polymorphism, with euphallic, hemiphallic and aphallic individuals.

Shell (Text-fig. 10 I)

Relatively short and broad.

Pallial organs (Text-fig. 10 D)

As in *A. reticulatus.*

Retractor muscles (Text-fig. 11 F)

The cephallic retractor muscles arise by a long common stem, and so are less deeply divided than in the other species. The retractor penis is occasionally absent.

Nervous system

As in *A. reticulatus.*

Jaw

Pale golden, 1 mm across.

Radula (Text-fig. 11 N)

Rather fewer lateral teeth, and small ectocones on more of the external marginals, than in *A. reticulatus* and *A. agrestis*. Formula C.13.26.

Alimentary system

The rectum lacks a caecal diverticulum, as in *A. caruanae*. The visceral cavity is often somewhat pigmented, though less so than in *A. caruanae.*

Reproductive system (Text-figs. 11 A and B)

The dark ovotestis is less exposed than in the other species. The hermaphrodite duct is short and nearly straight, with the usual seminal vesicle at the short brown albumen gland. The female portion of the common duct is leaden grey, and the prostate yellow. The spermatheca is normally oval as in the other species, but sometimes in young examples it is globular. The penis in a euphallic individual shows four regions: a distal, narrower segment; a wider one enclosing the triangular sarcobelum; a twisted and contorted segment entered distally by the vas deferens, and giving attachment to the retractor penis; and a short narrower segment (diverticulum or appendix), more or less bifid at the tip. The appendix contains two thickened pilasters, which fade out on reaching the sarcobelar segment. In the aphallic form (Text-fig. 11 B) prostate and spermatozoa are present, but the vas deferens fades out or ends in a little vesicle, before reaching a minute knob representing the penis. Apparently the penis is always the last part to be fully developed; but in young examples that will become euphallic the vas deferens does reach the small penis and a retractor muscle is often present. Stages can be found between this and the adult euphallic form. Babor (1894) records observations which he thought indicated that *A. laevis* was normally protogynous—young adults being always female and middle-aged adults hermaphrodite, with some old animals attaining a purely male phase, with atrophied albumen gland and spermatheca and hypertrophied penis. He states that in the young stages sperms are very few, and there is no sperm duct or penis. However, dissection of many British examples, taken at various sites and different seasons, shows that here sperms, prostate and vas deferens are always present; though in animals that will eventually be aphallic the vas deferens ends blindly. No example has been seen in which the albumen gland and spermatheca have atrophied. As these forms often occur together, in varying proportions in the same site at different seasons, it seems more likely that this is a case of genital dimorphism, such as occurs in *Zonitoides*. To establish this with certainty it is desirable that samples should be taken from the same site each month for a year, but an opportunity to do this has not occurred. Pilsbry (1948: 539–552) gives numerous figures of similar dimorphism in the American forms of *A. laevis*.

Mating

Gerhardt (1939) says that following and circling around is omitted in *A. laevis*, and that the partners remain in contact before the sperms are transferred for a much longer period (up to an hour) than in the other species.

Development

The eggs are laid singly or in small clusters, probably at all seasons of the year, having been found in January, April and October. They are relatively large, from 1·8 × 1·5 to 2 × 1·3 mm, translucent, resilient, finely punctate, with polygonal calcareous granules. They hatch in four or five weeks. The young are 4 mm long, white and translucent, with the opaque white liver lobes showing through the integument. The head and tentacles are light pinkish-brown with a violet tinge.

After a few days, pigmentation begins at the tail and head, and gradually invades the rest of the body.

Ecology

A. laevis inhabits damper sites than our other slugs and is common in marshes and on the borders of ponds and rivers, but is occasionally found in drier sites, in fields and on the borders of woods. It has been seen feeding on mealy bugs infesting *Streptocarpus* in greenhouses.

Distribution (Map 17)

Probably ubiquitous in the British Isles. Its continental distribution is somewhat uncertain, because of the existence of a somewhat similar slug distinguished by a hammer-headed penis (p. 172). It is common in marshy places throughout the Holarctic, extending southwards in Europe to northern Italy. Most of this range is probably occupied by the true *A. laevis*, showing only slight infra-specific variation. *A. laevis* has been widely introduced into tropical regions and oceanic islands, where it has been recorded under many different names. For example, specimens from Hawaii in the B.M. (N.H.) labelled as *A. bevenoti* Collinge (Kauai) appear to belong to the aphallic form of this species, and others labelled as *A. perkinsi* Collinge (Lanai) and *A. globosus* Collinge (Mauna Loa) to the euphallic form.

Fossil record

Pleistocene to Recent.

Material examined

Living specimens from many places in England and Wales. Spirit specimens from the type locality (Frederiksdal, Denmark), kindly collected and sent to me by Dr. Mandahl-Barth, and from Britain, South America, New Zealand and Hawaii.

Agriolimax caruanae Pollonera, 1891

Agriolimax caruanae Pollonera, 1891 : 3. Porta Reale, Malta.

Notes

Pollonera described the keel of his species as blackish, and figured a more globular spermatheca than is found in adult British specimens. However, in Britain the keel and head are the first parts to pigment, so that in young animals they are darker than the rest of the body. The spermatheca is sometimes globular, in young animals at any rate in Britain, and in adults of some American forms. Pilsbry (1948 : 558) figures considerable variation between American specimens, which he nevertheless recognizes as belonging to *A. caruanae*. The British slug can be at most a geographical race of this species, of which Quick (1949 : 28) gives a short account.

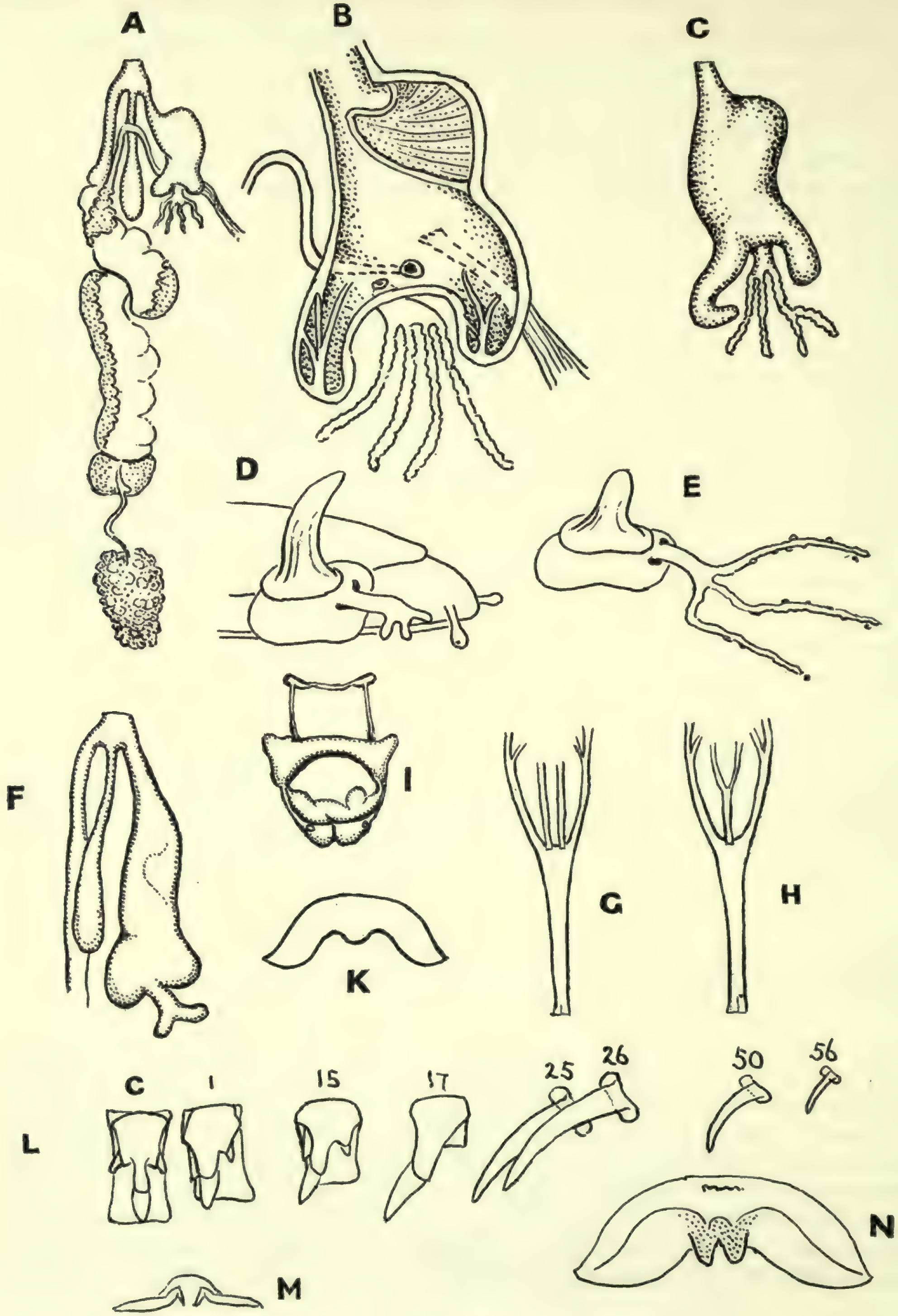
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Fig. 12.

First British record

Specimens, found by the late Charles Oldham in Cornwall about 1930, were identified with this species (as perhaps a distinct subspecies or variety) by H. Watson, and exhibited at meetings of the Conchological Society of Great Britain and Ireland and the Malacological Society of London.

Diagnostic features

Distinguished in life from the externally similar *A. laevis* by larger size and even greater activity. Internally distinguished by having two penial diverticula and a tuft of appendages, a darkly-pigmented visceral cavity, and a greater number of marginal radular teeth.

External appearance (Pl. 2, fig. 17)

The length when extended is 2·5–3 cm, or a little more. As in *A. laevis*, the head and neck extend far beyond the mantle. The slug is dark translucent chestnut brown, greyish-brown or grey, with the mantle lighter over the pallial region, and the body and mantle more or less flecked with dark brown. The respiratory orifice is pale rimmed. The sole is grey rather than brown, because the dark visceral pigmentation shows through the tissues. The mucus is thin and colourless.

External variation

The colour varies from a clear chestnut-brown to a greyer brown, and the small darker flecks on body and mantle are more or less marked, but there are no named varieties.

Shell (Text-fig. 10 H)

4·5 × 2 mm, or a little larger. In undistorted specimens, the right border is slightly concave.

Pallial organs (Text-fig. 10 E)

As in *A. reticulatus*.

FIG. 12. *Agriolimax caruanae.* **A.** Reproductive organs (× 4). **B.** Penis (× 14) opened to show sarcobelum, two diverticula, entries of vas deferens and crenulate branched appendix, penial retractor. **C.** Penis (× 8). **D.** Sarcobelum protruded, atrium everted, appendix beginning to be everted. **E.** Three branches of appendix fully everted, sarcobelum beginning to shrink. **F.** Distal genital ducts (× 30) of young individual 11 cm long, showing oviducts, spermatheca, sarcobelum in penis, rudiments of diverticula and appendix. **G & H.** Cephalic retractors. The buccal retractor is sometimes completely divided. **I.** Ganglia and commissures of nerve ring. **K.** Jaw (× 20). **L.** Representative radular teeth (× 500). **M.** Jaw (× 100) of individual one day old. **N.** Jaw (× 100) of young individual 6 mm long.

Retractor muscles (Text-figs. 12 G and H)

The cephalic retractors arise by a common stem, and the buccal retractor is divided either completely or for half its length.

Nervous system (Text-fig. 12 I)

As in *A. reticulatus*.

Jaw (Text-fig. 12 K)

Of the usual oxygnathous type, 1·3 mm across. In the newly-hatched animal, a median indentation (like that seen in *Milax*, *Limax* and *Vitrina*) reveals a bilateral origin (Text-figs. 12 M and N).

Radula (Text-fig. 12 L)

Characterized by having rather fewer lateral teeth and more marginals than *A. reticulatus* and *A. agrestis*. Formula C.14.55.

Alimentary system (Text-fig. 10 C)

As in *A. laevis*, there is no rectal caecum. The walls of the visceral cavity are darkly pigmented.

Reproductive system (Text-figs. 10 C and 12 A–F)

The dark ovotestis lies rather far forwards, and is partly exposed on the left side of the visceral mass. The oviduct, atrium and spermatheca require no special comment. The basal segment of the penis is slender and the segment containing the sarcobelum capacious. The distal segment bears apically two curved hollow processes, of which the left is often the longer, and between these an appendix with four or five long slender crenulated branches, corresponding with the apical appendix of *A. reticulatus*.

Mating (Text-fig. 10 K)

Breeding occurs throughout the year, eggs having been seen in January, May, June, July, October, November and December. A mating pair was observed on 25th June, 1950. At 6.10 p.m. the partners were following one another in a circle, with protruded sarcobela, licking one another's tails. At 6.40 they were lying quietly with their necks close together, with the atria everted and the sarcobela shrinking. A few seconds later, the four long tubular branches of the penial appendices were everted, lying across the partner's body like hyaline threads. At 6.42 the everted organs were rapidly withdrawn, with the sarcobela last, and the animals crawled apart.

Individuals from Glamorgan and Denbigh, isolated from birth, have on several occasions been seen to lay a few self-fertilized eggs, which have developed to an advanced stage although they have not been seen to hatch. Gregg (1944) reports fertile eggs from virgin specimens in California. There this species (for which Gregg uses the name *Deroceras panormitanus*) apparently passes through a purely female phase when about half grown. Only about half the individuals survive this phase, to grow to full size and develop male organs. There is no sign of such a female phase in Britain, where slugs only 10 mm long, with their common ducts still slender and immature, always have penes in which the rudiments of all the adult features are easily recognizable. Two diverticula, a budding tufted appendix and a sarcobelum can be seen in a penis between 1·3 and 1·6 mm long. Aphallic and hemiphallic individuals are unknown in Britain. In any case, aphallic individuals of *A. laevis* are not in a female phase, since they have spermatozoa and a prostate. Gregg's observations are explicable in two ways : he may possibly have been working with a mixed culture of *A. caruanae* and *A. laevis*, or the difference may be related to the more rapid development of *A. caruanae* in California than in Britain.

Development

The eggs are relatively small, from 1·5 × 1·5 to 1·75 × 1·4 mm : much smaller than those of *A. reticulatus* and *A. agrestis*, and not much larger than those of *A. laevis*. They are laid in clusters of up to fifty eggs, and in the summer hatch in about seventeen days. The young are only about 3 mm long, very pale and translucent, with pale violet tentacles. Pigmentation begins at the head and tail, as in *A. laevis*.

Behaviour

A. caruanae crawls extraordinarily fast for a slug, and is irritable and pugnacious, snapping at its neighbours and lashing its tail. Even when well supplied with food, it shows cannibalistic tendencies.

Ecology

Usually confined to gardens, in flower and vegetable beds, lawns, rubbish heaps and greenhouses ; but occasionally found at a distance from houses, in hedges, fields and waste places (records from Devon and Glamorgan).

Distribution (Map 18)

Recorded from scattered localities in England (mainly in the west), Wales, Scotland and southern Ireland (Makings, 1959). The extra-limital distribution is very imperfectly known. Repeated efforts to obtain topotypes from Malta have failed. The species probably occurs at Marseilles (Pilsbry, 1948 : 560), and has been introduced into California.

Fossil record

Holocene shells from Romney Marsh (Hayward, 1954*a* and *b*) are very suggestive of this species. Although slug shells are badly characterized, especially when fossil, there is a prima facie case for believing that these are indeed shells of *A. caruanae*. Otherwise, the species is known only from Recent deposits.

Material examined

Living or spirit specimens from St. Agnes, Scilly Isles ; Exeter, Devon ; Swansea and Porteynon, Glamorgan ; Old Colwyn, Denbighshire ; St. Albans, Hertfordshire ; Bromborough, Cheshire ; Edinburgh and Aberdeen, Scotland ; Cork (grounds of the University, from Dr. Makings) and Newcastle, Co. Down (Dr. Stelfox's garden), Ireland ; Pyrenées Orientales ; Golden Gate Park, San Francisco.

Genus ***LIMAX*** Linnaeus, 1758

Type species *Limax maximus* Linnaeus, 1758.

Limacinae in which the right ocular retractor passes forwards between the penis and the vagina. The intestine has two forwardly-directed loops, and the left lobe of the liver forms the apex of the visceral mass. There is no penial stimulator. The nucleus of the concentric mantle ridges lies in the mid-dorsal line. The dorsal keel slopes evenly to the end of the tail, which is therefore pointed and not truncated.

Hesse (1926 : 8–16, 76–92) divides *Limax* into several subgenera, and the nominate subgenus into sections. Since no regular trends in several characters are discernible, each species being specialized in some respect or another (e.g. the long penis and peculiar mating behaviour of *L. maximus* and *L. cinereoniger*), the infrageneric arrangement depends largely on the relative systematic importance attached to the radula, penis, alimentary tract and other organs. For example, *L. nyctelius* may be associated with *L. flavus* in the section *Limacus*, on the basis of its rather long cylindrical penis and long rectal caecum ; but their radulae are very different, that of *L. flavus* being specialized in the suppression of ectocones and endocones, while that of *L. nyctelius* approaches the condition of *Agriolimax*. Subgeneric and sectional names are therefore not adopted here.

Limax tenellus Müller, 1774

Limax tenellus Müller, 1774 : 11. Denmark.
Limax tenellus; Nilsson, 1822 : 11.
Limax serotinus Schrank, 1848 : 144.
Limax cereus Held, 1849 : 15.
Limax fulvus Normand, 1852 : 7.
Agriolimax tenellus; Lessona & Pollonera, 1882 : 45, pl. 1. fig. 7.

Notes

Although Nilsson is often quoted as the author of this name, it was first applied by Müller. Ignoring an obvious mistake in measurement, Müller's description seems adequate to identify the present species : " Limax virescens, capite tentaculisque nigris. Dan. SPÆD-SNEGLEN. long. 10 unc. Totus albidus, *Clypeus* in luteum, abdomen in virescentem colorem aliquantum vergit ; ille margine postico, hoc apice supra nigricat. In Fossulis Nemorum foliis aridis repletis ; primo vere."

Altena (1958) confirms that *L. fulvus* Normand is indeed *L. tenellus*.

First British record

By Alder (1848 : 124).

Diagnostic features

Distinguished externally from other British species by small size, and pale yellow colour, with black head and tentacles; and internally by a short penis with no appendix.

External appearance (Pl. 2, fig. 16)

The smallest British *Limax*, from 25 to 35 mm long when extended. Colour pale yellow, or sometimes reddish-brown, with blackish head and tentacles, and sometimes with a pair of more or less distinct body and mantle bands. The mucus is yellow.

External variation

Var. *cerea* Held (1849), uniform yellow, or with mere traces of bands; var. *fulva* Normand (1852), reddish-brown, suffused dorsally with black; var. *cincta* Heynemann (1861), with distinct dark mantle bands, and sometimes body bands.

Shell

Thin and delicate, measuring about 3·5 × 2 mm.

Pallial organs (Text-fig. 13 D)

The somewhat angularly crescentic kidney partly embraces the heart and pericardium, just behind the origin of the penial retractor.

Retractor muscles (Text-fig. 13 E)

The cephalic retractor arises by two roots in the mid-dorsal line just behind the kidney, and divides about half-way along into right and left tentacular retractors. The right tentacular retractor passes forwards between the penis and oviduct, and not on the left of both as it does in *Milax* and *Agriolimax*. The pharyngeal retractor arises half-way along the left tentacular retractor, and divides into right and left branches passing to the buccal bulb between the cerebral and visceral ganglia. The penial retractor arises from the diaphragm on the left side, in front of the pericardium.

Nervous system (Text-fig. 13 H)

The olfactory and optic lobe of the cerebral ganglion is large, the cerebro-pleural and cerebro-pedal commissures short, and the visceral ganglia closely approximated, the right visceral and abdominal ganglia being fused together.

Jaw (Text-fig. 13 F)

Of the usual oxygnathous type, 1·5 mm across.

Radula (Text-fig. 13 G)

The central tooth, 0·038 × 0·018 mm, with small but distinct ectocones, is flanked on each side by about twenty lateral teeth with both ectocones and endocones, followed by about forty-five marginal teeth. The teeth between the eighteenth and twenty-second are transitional in character, the endocone diminishing, and the ectocone approaching the mesocone. In the marginals, the mesocone becomes relatively longer and more curved, and the ectocone becomes prominent, arising from the side of the mesocone. Ectocones occur in some of the outer marginals of other *Limax* species, but they are not the conspicuous feature throughout that they are in *L. tenellus*. Formula C.20.45 × 110.

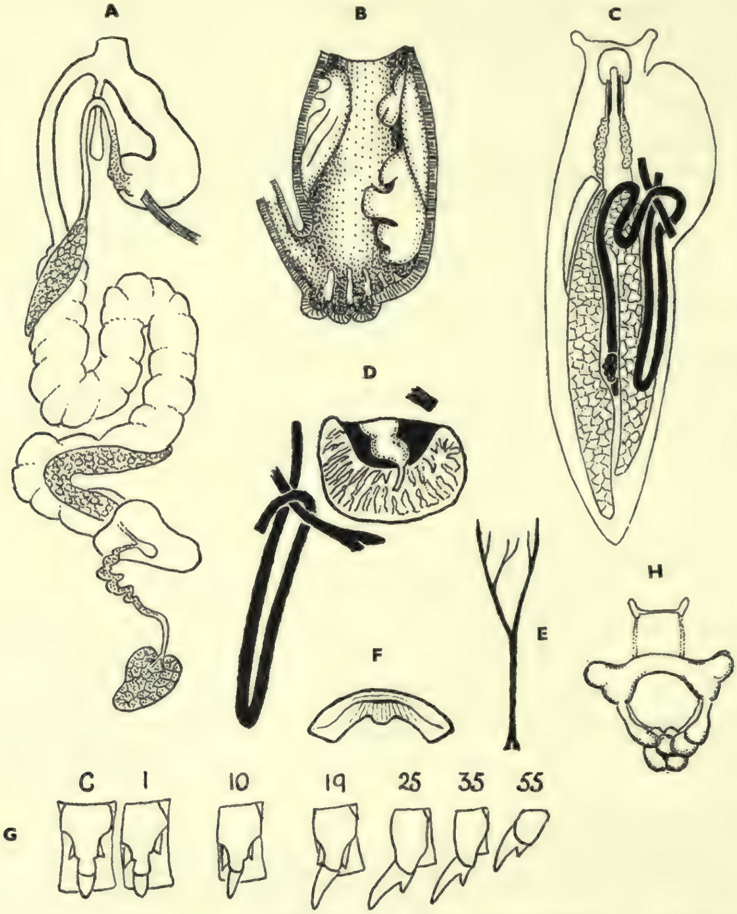


Fig. 13. *Limax tenellus*. **A.** Reproductive organs (× 4). **B.** Penis (× 6·7) opened. **C.** Alimentary system, showing left lobe of liver forming apex of visceral mass, ovotestis at stomach level, between left and right lobes, intestine, cephalic retractor, oesophagus, salivary glands, buccal bulb, portion of albumen gland below left liver lobe. **D.** Kidney, heart and pericardium, origin of penial retractor in front, second forwardly-directed loop of intestine passing around cephalic retractor, rectum. **E.** Cephalic retractor muscles. **F.** Jaw (× 14). **G.** Representative radular teeth (× 330). **H.** Nerve ganglia (× 8).

Alimentary system (Text-fig. 13 C)

The left lobe of the liver forms the apex of the visceral mass. The apex of the stomach forms the most posterior part of the alimentary tract (which in *Limax* has almost lost the spiral torsion seen in *Arion* and in *Milax*), and the intestine has two forwardly directed loops. The first of these is held in place by the aorta as usual, and the second, which extends further forwards, is crossed by the cephalic retractor. The intestine runs backwards from this point and turns sharply to run forwards as the rectum, between the cephalic retractor and the floor of the pulmonary chamber, to the posterior lip of the respiratory orifice.

Reproductive system (Text-fig. 13 A)

The darkly pigmented ovotestis lies behind the stomach, but a little of it may be visible from the dorsal aspect, between the right and left lobes of the liver. The dilated central part of the hermaphrodite duct is pigmented and sinuous, narrowing at the albumen gland, where it has a distinct unpigmented vesicula seminalis. The prostate does not diverge anteriorly from the oviduct. The short vas deferens, which is not bound down by the right ocular retractor, becomes sacculate and pigmented at the entrance to the penis, apically above the insertion of the penial retractor. Internally the penis (Text-fig. 13 B) shows three or four delicate short transverse folds apically, and further forwards three main massive longitudinal folds, the exact appearance varying according to where the penis is opened. These folds are visible during copulation (see below). The spermatheca is small and club-shaped, with a short duct entering the atrium.

Mating

According to Gerhardt (1933 : 445), one animal follows the other rapidly, head to tail. The leader soon bends to the right, so that after ten minutes the circle is completed. The penes are suddenly everted as massive bluish-white bodies, each with a thickened oblique fold which Gerhardt calls the comb. The penes are closely apposed, but not entwined, and the animals slowly revolve clockwise for one and a half hours. *L. tenellus* differs from *L. maximus* and *L. cinereoniger* in not entwining the body nor hanging from a horizontal surface.

Development

The eggs vary from 3·6 × 3·1 to 3·3 × 3·0 mm, and are pale amber, soft, translucent and slightly adherent. In Britain, they are laid from November to March in clusters of about fifteen, and take from sixty to 120 days to hatch. The young are 6 mm long, with a slight dorsal keel posteriorly. They are white and translucent, without body and mantle bands and with a more opaque kidney region. The tentacles are pale violet, with the dark brown retractor muscle showing through.

Ecology

Restricted to woodlands, usually of considerable extent, and one of the few slugs found in pine woods. Absent from most of the many woods and plantations established during the seventeeth century, which suggests that its powers of dispersal are poor. Indifferent to the presence or absence of lime.

Distribution (Map 19)

Of very local occurrence, though wide range, and therefore seldom encountered. In Britain, recorded from many vice-counties. In Europe, found from France northwards to Jemtland, and eastwards to the Caucasus.

Material examined

Living specimens from Netley Heath, Shere, Surrey; and Chepstow, Monmouthshire. Spirit specimens from Britain and Switzerland.

Limax flavus Linnaeus, 1758

Limax flavus Linnaeus, 1758 : 652. Sweden.
Limax variegatus Draparnaud, 1801 : 103.
Limax megalodontes Quoy & Gaimard, 1824 : 426.

First British record

By Lister (1685–97, pl. 101*b*).

Diagnostic features

Tentacles steely blue, body and mantle with yellowish spots and no lateral bands. Long rectal caecum and long cylindrical penis—a diagnostic combination for British *Limax*.

External appearance (Pl. 2, fig. 22)

A rather large slug, from 7 to 10 cm long when extended. Colour from yellowish to greenish, more or less suffused with dusky pigment, and mottled on the mantle with yellow patches, on the body with yellow spots formed by groups of up to seven tubercles. There are no lateral bands. The tentacles are a very characteristic cold steely blue, the sole pale yellow, the respiratory orifice pale-rimmed, and the mucus yellow.

External variation

Var. *rufescens* Moquin-Tandon (1855), reddish-brown; var. *virescens* Férussac (1819), uniformly greenish; var. *antiquorum* Sowerby (1834 ?), pale ochraceous marbled with grey; var. *breckworthiana* Lehmann (1864), uniformly suffused with dark pigment.

Shell

Rather large, 9 × 6 mm, thin and convex, with the nucleus near the posterior margin and a little to the left of the mid-line.

Pallial organs

As in *L. tenellus.*

Retractor muscles (Text-fig. 14 D)

The cephalic retractors arise from two roots, which do not unite for a considerable distance. The buccal retractor arises near the origin of the left ocular retractor. The penial retractor arises from the diaphragm, in the region of the kidney.

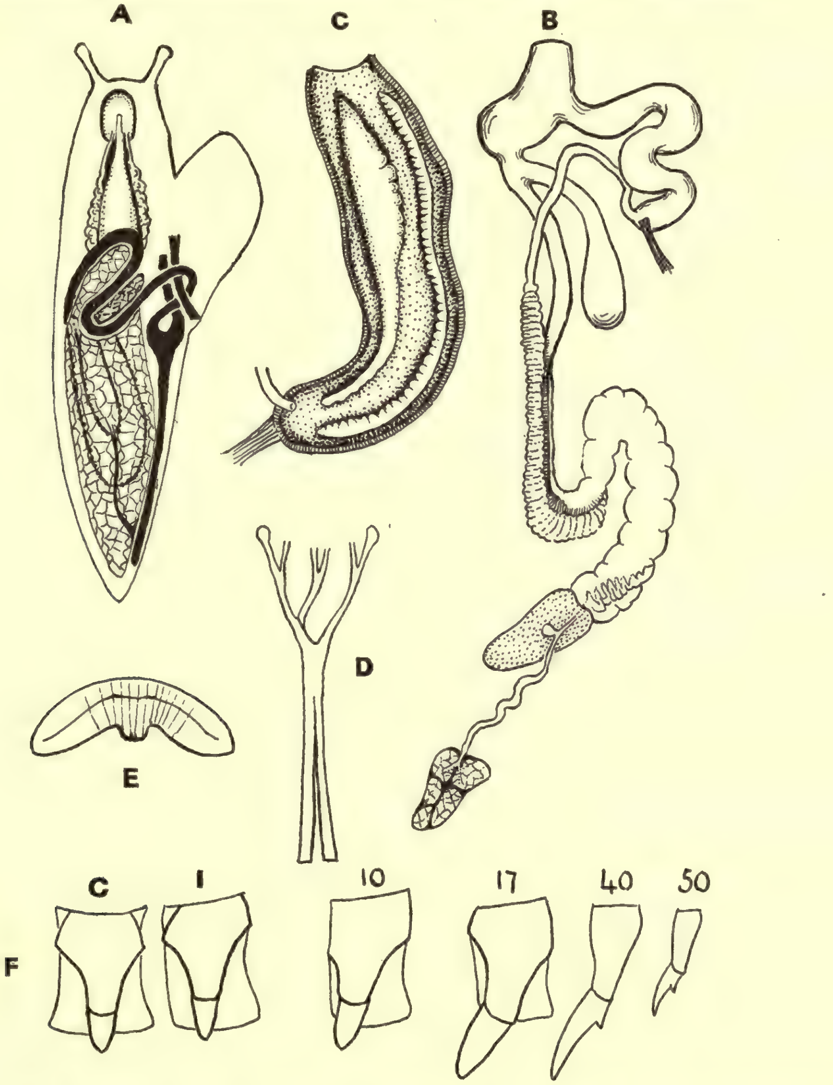


FIG. 14. *Limax flavus.* **A.** Alimentary system (× 2) showing second forwardly-directed loop of intestine passing around cephalic retractor, long rectal diverticulum passing backwards. **B.** Reproductive organs (× 2). **C.** Penis (× 6) opened to show internal folds. **D.** Cephalic retractor muscles. **E.** Jaw (× 14). **F.** Representative radular teeth (× 330).

Nervous system

As in *L. tenellus*.

Jaw (Text-fig. 14 E)

2·25 mm across, dark brown in colour. Marked transversely with fine striae, which are crossed by still finer ones following the contour of the jaw.

Radula (Text-fig. 14 F)

Measures 6·5 × 2·6 mm, with about 150 rows of teeth. The central tooth (measuring 0·05 × 0·038 mm) has a strong mesocone, but its ectocones are obsolete or absent. The lateral teeth are also devoid of ectocones and endocones. The aculeate marginals, some of the outermost of which have small ectocones, are connected to the laterals by several transitional teeth. Formula C.16+4.50 × 150.

Alimentary system (Text-fig. 14 A)

The oesophagus dilates to a capacious crop, flanked by the salivary glands, and merging gradually into the stomach. The second forwardly directed loop of intestine is held in place by the cephalic retractor muscle. Instead of being prolonged backwards as it is in *L. tenellus*, it soon turns forwards as the rectum ; but from the apex of the bend a long rectal diverticulum extends backwards, on the surface of the liver, to the end of the body. As in the other species of *Limax*, the left liver lobe forms the apex of the visceral mass.

Reproductive system (Text-fig. 14 B)

The unpigmented ovotestis lies between the lobes of the liver, well below the stomach apex. The hermaphrodite duct, at its entrance to the yellow linguiform albumen gland, has a rounded white seminal vesicle. The ribbon-like yellow prostate diverges from the oviduct anteriorly, and can easily be peeled off it for the greater part of its length. The vas deferens runs forward, and turns back beneath the right ocular retractor to the apex of the penis. The penis is a rather long cylindrical organ, strongly folded in a spiral. Internally it bears (besides three or four minor longitudinal folds) a long, low, crinkled, ribbon-like fold along its whole length, and another more prominent fold that expands distally to a crest or " comb ", lobulated or crenulated on the free margin (Text-fig. 14 C). The oviduct expands at its entrance to the atrium, where the spermatheca arises from it.

Mating

Mating occurs from late summer to February. According to Gerhardt (1933), after " following " for about eight minutes, the animals approximate the right sides, but do not curve into a circle. The penes are rapidly everted and entwine spirally, forming a mass of about one square centimetre in area. Sperms enclosed in a mucous mass are transferred between the penes, which are rapidly withdrawn carrying the partner's sperms with them. The whole process occupies only half a minute. Gerhardt does not state what follows, but presumably the sperms are transferred from the withdrawn penes to the spermathecae.

Development

The eggs are laid in clusters of up to twenty, and have been found in September and February. They are large, 6 × 4 mm, pale amber in colour, and differ from those of other British slugs in having a small rounded projection at each end, so that they resemble miniature lemons. They hatch in from three to six weeks at room temperatures. The newly-hatched young are from 10 to 13 mm long, pale greenish-yellow with the characteristic blue tentacles already evident. There are no bands at any stage, and the yellow spots of the adult appear later in development.

Behaviour

L. flavus is essentially nocturnal, and unless looked for after dark it may escape observation in urban surroundings, even where it is abundant.

Ecology

L. flavus is found in woods, under logs and bark, but is much commoner in gardens, in the crevices of walls, and in cellars and out-houses. It eats decaying vegetable matter, fungi and lichens in wild places, and mildew and garbage in gardens and out-houses.

Distribution (Map 20)

Probably occurs in every vice-county of the British Isles, and ranges from southern Norway to North Africa and eastwards to Syria. It has been introduced into South Africa, Australia and North and South America, and to islands in the Atlantic and Pacific.

Material examined

Living specimens from Swansea, Glamorgan; and Reading, Berkshire. Spirit specimens from Britain, Corsica, Greece, North and South America, South Africa, Australia, and the New Hebrides and Cook Islands.

Limax cinereoniger Wolf, 1803

Limax cinereoniger Wolf, 1803 : 7. Germany.
Limax antiquorum Férussac, 1819 : 68 (in part).
Limax maximus; Gray, 1840 : 113 (in part).
Arion lineatus Dumont, 1850 : 64.
Limax cinereus var. *intermedia* Brevière, 1881 : 314.

First British record

By Gray (1840).

Diagnostic features

Largest British slug, usually black with dorsal line and median zone of sole white, keel prominent and rather long. Distinguished from *L. maximus* by coloration, and by coarser tubercles, spotted tentacles, relatively small shell and jaw, and longer penis not tapering distally.

External appearance (Pl. 2, fig. 25)

This is our largest native slug, which grows to 10 or 20 cm long in this country, while some continental forms are even larger. The keel is prominent and long, and the tubercles relatively coarser than in *L. maximus*. The slug is usually black all over, except for the white mid-dorsal line and median area of the sole. The dark tentacles are spotted with small discrete black or dark brown dots—a character distinguishing the species from *L. maximus*, which has apparently not been recorded previously.

External variation

In Britain the ground colour, seen in the mid-line and the median area of the sole, is usually whitish, but in continental specimens the keel may be red or yellow. The following named varieties have been recorded from Britain: var. *ornata* Lessona (1880), body black with a series of white spots along each side; var. *maura* Held (1836), entirely black; var *cinerea* Moquin-Tandon (1855), entirely ash-coloured except for bluish-black mantle; var. *punctata* Lessona (1880), keel and mid-line of dorsum yellow, two interrupted bands on each side.

Shell

Relatively smaller (9 × 5 mm), thinner and slightly more elongated than that of *L. maximus*.

Pallial organs

As in *L. tenellus*.

Retractor muscles

The slender cephalic retractor arises from the mid-line behind the diaphragm, and crosses the second forwardly-directed intestinal loop. The right ocular retractor passes (as is usual in *Limax*) between the male and female divisions of the distal genital ducts, over the vas deferens. The penial retractor arises broadly from immediately to the left of the cephalic retractor, and narrows to its insertion at the apex of the penis.

Nervous system

As in *L. tenellus*.

Jaw (Text-fig. 15 E)

Usually about 3 mm across, but may reach 4 mm in very large specimens: relatively smaller than in *L. maximus*.

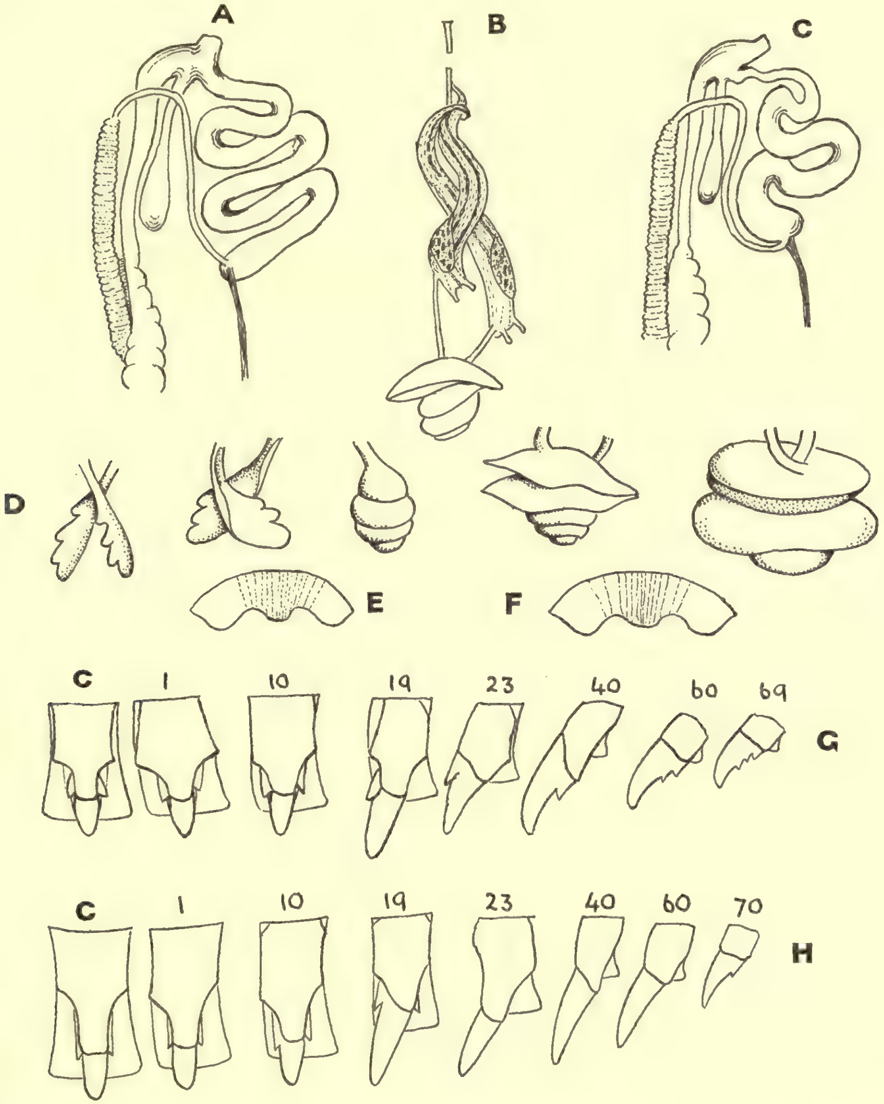


Fig. 15. *Limax.* A. *L. cinereoniger*—distal genital ducts (× 1·3). B. *L. maximus*—mating pair suspended from mucus thread (adapted from L. Adams). C. *L. maximus*—distal genital ducts (× 2). D. *L. maximus*—stages in eversion and entwining of penes (adapted from L. Adams). E. *L. cinereoniger*—jaw (× 6·7). F. *L. maximus*—jaw (× 6·7). G. *L. cinereoniger*—representative radular teeth (× 330). H. *L. maximus*—representative radular teeth (× 330).

Radula (Text-fig. 15 G)

There are about 150 rows of teeth. The central tooth has rather small but strong ectocones. It is flanked by about nineteen laterals, with ectocones and endocones, the latter descending on the mesocones in the outer teeth. There are about fifty marginals on each side, of which only the inner teeth retain the endocone. In the outer marginals, an ectocone appears on the concave side of the mesocone, and becomes bifid or trifid in a few of the outermost teeth. Formula C.19.50 × 150.

Alimentary system

Resembles *L. tenellus*, and differs from *L. flavus*, in having the loop of intestine which is retained by the cephalic retractor prolonged backwards almost to the visceral apex, and without a rectal caecum. The loop is longer than in *L. maximus*.

Reproductive system (Text-fig. 15 A)

The long narrow darkly pigmented ovotestis is visible on the surface between the left and right liver lobes. The hermaphrodite duct is pale, slender at first, then wider and folded, and narrows at the somewhat triangular albumen gland. If a seminal vesicle is present, it is small, deep in the albumen gland and difficult to find. The folded common duct narrows to a long free oviduct, dilated at its entry into the atrium, and the small club-shaped spermatheca arises one or two millimetres before its end. The prostate separates from the common duct and so is free at its anterior end, and the vas deferens passes under the right ocular retractor and back to the apex of the penis. The stout cylindrical contorted penis is of nearly uniform diameter throughout its length, and when straightened out is from 6–8 cm long. Internally it bears a prominent fold, double at its origin. In its upper part this expands into a prominent frill, the " comb ". The rest of the mucous membrane is circularly ridged.

Mating

Mating occurs at night, throughout the milder periods of the year, on vertical or overhanging surfaces. After about fifteen minutes of " following ", the animals hang down freely from a disk of mucus. Their bodies and the evaginated penes, which become as long as the bodies, are entwined. A mass of sperms enclosed in mucus descends each vas deferens inside the penis, and the sperm packets are exchanged between the " combs " which are now terminal. The penes are then withdrawn, carrying the sperms with them to be transferred later to the spermathecae. The whole process takes about twenty minutes.

Auto-fecundation can occur in this species (Oldham, 1942*a*).

Development

The eggs are about 5 × 5·5 mm, soft, translucent and amber-coloured. On account of the large size of the eggs, and their transparency when under water, the caudal and cephalic vesicles of the embryos can easily be observed (Text-fig. 18 H). The eggs hatch in about a month. The newly hatched young are translucent white, but soon become opaque, then brown and finally black. There is sometimes a suggestion of banding, and the lateral areas of the foot are the last to pigment.

Oldham (1942*a*) records that this slug becomes mature in two years, and that an individual in captivity lived for five years and 270 days.

Ecology

This is essentially a slug of wild places, being found beneath logs and leaves and in tree crevices of ancient woodlands. In Pembrokeshire at least, it also occurs on damp lichen-covered rocks on bare hillsides. It seems never to occur in gardens and cultivated land or recent plantations. Though in the wild it presumably feeds on lichens, fungi and decaying vegetable matter, in captivity it readily eats carrot, oatmeal etc.

Distribution (Map 21)

L. cinereoniger is recorded from most British vice-counties, except for East Anglia and parts of central England, southern Scotland and central Ireland. In Europe, it extends from arctic Norway to north-eastern Spain, Italy, Sardinia, Greece and the Crimea.

Material examined

Living specimens from Netley Heath, Surrey ; Cusop Dingle, Hereford ; Bucklebury, Berkshire ; and Pont Neath Vaughan, Glamorgan. Spirit material from Britain, Denmark, Germany and Luxemburg.

Limax maximus Linnaeus, 1758

Limax maximus Linnaeus, 1758 : 652. Sweden.
Limax cinereus Müller, 1774 : 5.
Limax antiquorum Férussac, 1819 : 68 (in part).

First British record

By Lister (1674 : 99).

Diagnostic features

Large, differs from *L. cinereoniger* in coloration : grey or brown with two or three bands on each side of body, dark spotting or marbling on mantle, tentacles pale pinkish-brown without spots, sole uniformly pale ; and also in having the tubercles relatively smaller, the shell and jaw relatively larger and the penis shorter and tapering distally.

External appearance (Pl. 2, fig. 24)

Length from 10 to 20 cm. The tubercles are relatively smaller than in *L. cinereoniger*. The slug is usually some shade of grey, with a uniformly pale sole.

The body bears two or three bands, often doubled or more or less interrupted, on each side. The mantle is irregularly spotted or marbled with dark pigment, but never banded. The tentacles are translucent pinkish-brown, without spots.

External variation

The ground colour may be grey, ochraceous or reddish, and the bands may be developed to an infinitely variable degree. Named varieties are: var. *concolor* Pini (1876), uniformly ash-coloured; var. *candida* Lessona & Pollonera (1882), white, translucent, eyes pale brown; var. *vinosa* Baudon (1884), purple or vinous brown; var. *fasciata* Razoumowsky (1789), ash-coloured with three bands on each side; var. *sylvatica* Morelet (1845), ash-coloured with two bands, and an indistinct third lower band; var. *tetrazona* Taylor (1902), with only two bands on each side; var. *cellaria* Dezallier d'Argenville (1742), bands interrupted; var. *aldrovandi* Moquin-Tandon (1855), ash-coloured with pale spots; var. *tigris* Taylor (1902, from Adams MS.), tawny yellow with black bands.

Shell

Measures about 11 × 7 mm, and is thus relatively larger than that of *L. cinereoniger*.

Pallial organs, retractor muscles, nervous system

As in *L. cinereoniger*.

Jaw (Text-fig. 15 F)

Relatively larger (3·5 mm across) than that of *L. cinereoniger*.

Radula (Text-fig. 15 H)

The central tooth is larger and relatively narrower than in *L. cinereoniger*, and its ectocones are more delicate and sometimes almost obsolete. There are about nineteen lateral teeth on each side, all or most of which retain both ectocones and endocones. The marginals (about fifty on each side) lack endocones, and only some of the outermost teeth have small ectocones. Formula C.19.50.

Alimentary system

As in *L. cinereoniger*, except that the last posteriorly-directed loop of intestine is shorter, reaching only about half-way along the visceral mass. There is no rectal caecum.

Reproductive system (Text-fig. 15 C)

The ovotestis is of the same long flattened linguiform shape as in *L. cinereoniger*, but is pale or only slightly pigmented. The hermaphrodite duct, albumen gland, common duct, free oviduct and spermatheca are also similar. The distal end of the prostate diverges more or less from the oviduct, and above this the prostate is only weakly attached for a considerable distance. The penis differs from that of *L. cinereoniger* in being shorter, widest apically and tapering distally. Internally there is a fold, expanded proximally into a " comb ", as in *L. cinereoniger.*

Mating (Text-figs. 15 B and D)

This occurs at night from overhanging surfaces. Unlike *L. cinereoniger, L. maximus* hangs suspended in mid-air from a stout thread of mucus. The protrusion of the organs, sperm transfer, and withdrawal of the penes is as in *L. cinereoniger*, but the entwined penes are not so long. After withdrawal, the animals re-ascend the mucus thread. Adams (1898) gives further details.

Development

The eggs, 5·0 × 5·5 mm, resemble those of *L. cinereoniger*. They are laid in early spring and in the autumn. February eggs in an unheated room hatch in six and a half weeks. The young are pale grey, with the middle lateral bands visible from hatching—thus differing from young *Lehmannia marginata*, in which the upper band appears first and mantle bands are also present. The tentacles are pale pinkish-grey. After two or three weeks, the other body bands have appeared and begin breaking up, and the mantle becomes marbled.

L. maximus lives for at least three or four years.

Ecology

L. maximus occurs in woods, hedgerows and waste places, where it is sometimes found together with *L. cinereoniger* ; but unlike the latter it occurs also in gardens, cellars and out-houses. It seems to avoid green leaves and to feed on fungi and decaying matter, though in captivity it readily eats oatmeal, Bemax etc.

Distribution (Map 22)

Apparently general in the British Isles, and found from Oslo and Petrograd to Asia Minor, Algeria and the Atlantic isles. Introduced into North America, South Africa, Australia, Tasmania and New Zealand.

Material examined

Living specimens from Swansea, Glamorgan ; Savernake Forest, Wiltshire ; Bucklebury Common, Berkshire. Spirit material from Britain, France, Greece, Azores, Madeira, Canary Isles and British Columbia.

Genus ***LEHMANNIA*** Heynemann, 1861

Type species *Limax marginatus* Müller, 1774.

The penis is short, with a laterally-placed apical appendix (conical in *L. marginata*, short and cylindrical in *L. poirieri*, and long and cylindrical in *L. melitensis* Lessona & Pollonera). A long rectal caecum extends to the apex of the visceral mass. In

L. poirieri and *L. melitensis* the radula is like that of *Agriolimax*; but that of *L. marginata* is highly specialized. The body readily absorbs water and becomes swollen and translucent.

Hesse (1926) adopts sectional names within *Lehmannia*, segregating *L. marginata* (*Lehmannia* s.s.) from *L. poirieri* and *L. melitensis* (*Ambigolimax*) because of the former's specialized radula, although their reproductive and alimentary systems are very similar. As for *Limax*, subdivision of the genus depends on the importance ascribed to different characters.

Lehmannia marginata (Müller, 1774)

Limax marginatus Müller, 1774 : 10. Denmark.
Limax arborum Bouchard-Chantereaux, 1837 : 164.

First British record

By the Reverend B. J. Clarke (in Thompson, 1840 : 204).

Diagnostic features

Gelatinous aspect in damp weather, mantle bands forming lyre-shaped figure, two body bands on each side; conical penial appendix, rectal caecum, specialized radula.

External appearance (Pl. 2, figs. 18 and 21)

Usually about 7·5 cm long, or larger. Its great capacity for absorbing water makes this slug become semi-transparent and gelatinous in appearance during damp weather. When irritated, it exudes copious watery mucus. In colour it is characteristically grey with a pale sole, two darker body bands on each side (which may be more or less indistinct or interrupted), and a pair of mantle bands forming an elongated lyre-shaped figure. The keel is paler than the body, and the median area of the mantle often darker.

External variation

Var. *glauca* Clarke (1843), ground colour greenish-grey; var. *subrufa* Le Compte (1871), ground colour yellow; var. *rosea* Broeck (1870), ground colour pinkish; var. *bettonii* Sordelli (1870), body bands fused together and interrupted; var. *tigrina* Wienland (1876), with rows of black spots on body and mantle; var. *rupicola* Lessona & Pollonera (1882), darkly pigmented, with indistinct markings.

Shell

White and iridescent. Normally measures 4 × 2·75 mm, but varies considerably in size and thickness.

Pallial organs

As in *Limax*.

Retractor muscles (Text-fig. 16 c)

The main stem of the cephalic retractors arises from the mid-dorsal line just behind the kidney, and divides about half-way into the right and left ocular retractors. The buccal retractor arises from the left ocular retractor, a short distance in front of the bifurcation. The strong penial retractor arises from the diaphragm between the pericardium and the posterior border of the kidney, to be inserted below the vas deferens.

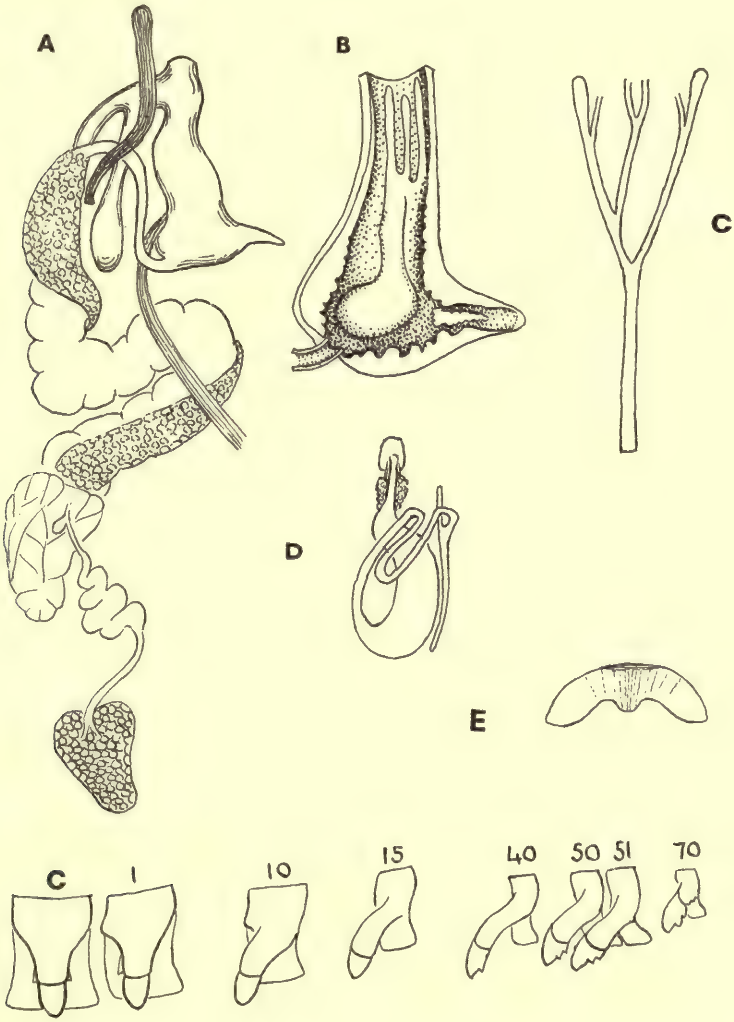


FIG. 16. *Lehmannia marginata.* **A.** Reproductive organs (× 3·3). **B.** Penis (× 5·3) opened longitudinally. **C.** Cephalic retractor muscles. **D.** Alimentary tract and salivary glands. **E.** Jaw (× 13). **F.** Representative radular teeth (× 330).

Nervous system

As in *Limax*.

Jaw (Text-fig. 7 E)

1·4 mm across, pale yellow in colour, and of the usual Limacid shape, not as narrow as figured by Taylor (1902–07, fig. 106).

Radula (Text-fig. 16 F)

Very characteristic, and easily distinguishable from the radulae of other British slugs. The central tooth has a strong, broad and short mesocone, and very small or obsolescent ectocones. It is flanked by ten or eleven laterals, with short wide mesocones and no ectocones, of which only the innermost one or two may have small endocones. The numerous marginals (up to seventy on each side) have characteristically strong, arched reflections bearing the short wide mesocones. From about the fortieth marginal outwards, the mesocone becomes bifid and then trifid, and minute denticulations corresponding to ectocones appear on the reflection.

Alimentary system (Text-fig. 16 D)

Resembles that of *Limax flavus*, with a rectal caecum extending backwards on the surface of the liver to the level of the stomach apex. The visceral cavity is darkly pigmented.

Reproductive system (Text-fig. 16 A)

The ovotestis is bulky and compact and superficially pigmented. The hermaphrodite duct is pale, swollen and folded in its median portion, and bears a rounded seminal vesicle where it terminates at the short linguiform albumen gland. The oviduct and spermatheca resemble those of *Limax*. The prostate is extraordinarily massive and deeply pigmented. The vas deferens, bound down by the right ocular retractor muscle, is short and wide, and enters the penis at the side of its blunt apex. At the opposite side of the apex there is a short conical appendix. The penis opened longitudinally (Text-fig. 16 B) shows a prominent fold, expanded and free at the apex and almost smooth, but corresponding with the " comb " of *Limax*. There is a small conical fold at the entrance to the appendix. The walls of the proximal part of the penis are thick and rugose.

Mating

This species can mate on level, vertical or overhanging surfaces.

Development

In Britain, mating occurs during the winter months. December eggs in an unheated room hatch in February. The eggs are soft, very translucent and pale amber in colour. They usually measure 4·3 × 3·6 mm, but some are smaller. The young are 10 mm long, pale translucent grey with violet tentacles. They show well-marked lyriform mantle bands, and a distinct band high up on the body—in contrast to young *Limax maximus*, in which the middle band is the first to appear.

Behaviour

Like many (perhaps most) slugs, especially when young, *L. marginata* is able to suspend itself from a mucus thread secreted by the pedal gland. This thread passes back along the foot to the tip of the tail and adheres to a branch or other object, and supports the animal when it crawls off. Sometimes the slug can even turn around and re-ascend the thread. Kew (1902) gives numerous examples of this process, with details and some figures.

Ecology

Not uncommon in old and newer woodlands, especially in the west and north. In dry weather it retreats into crevices in the bark and between roots, while in damp weather it crawls up the trunks to a height of twelve feet or more. It is also found on damp rocks on exposed hillsides, and on old stone walls.

Distribution (Map 23)

Probably occurs in every vice-county of the British Isles, but is commoner in the west and north. In Europe it is found from Iceland and Lapland to Russia and Italy, and is recorded as introduced into Australia and New Zealand. In North America, it apparently occurs wild at Torbay, Newfoundland (confirmed by Altena, 1950). However, introduced slugs from Verdugo Woodlands, Glendale, California, kindly sent by Dr. W. O. Gregg and recorded as this species, proved to be *L. poirieri*. Probably some of the records from southern Europe also refer to *L. poirieri*.

Material examined

Living specimens from the Gower Peninsula and the neighbourhood of Swansea, Glamorgan ; Brecknock ; Caernarvon ; and Torrington, Devon. Spirit material from Britain and Australia.

GREENHOUSE ALIENS

Lehmannia poirieri (Mabille, 1883)

? *Limax valentianus* Férussac, 1823, **2** : 96^{e}.
Limax poirieri Mabille, 1883 : 52. Spain.

Notes

A full list of references is given by Altena (1950 : 9–17).

First British record

By Quick (1949 : 24), as *L. valentianus*. However, Dr. A. D. J. Meeuse had already found it in a greenhouse in Belfast Botanical Gardens, on 26th November, 1948.

Diagnostic features

Somewhat like *L. marginata*, but the ground colour is yellower and paler, and the body bands nearer to the mid-dorsal line. The radula is like that of *Agriolimax*, very different from the specialized radula of *L. marginata*. The penial appendix is longer and more cylindrical than that of *L. marginata*, and not pointed at the apex.

External appearance (Pl. 1, fig. 14)

L. poirieri is about 6 cm long, with a yellowish-grey body and mantle, and slightly darker head. The general appearance is watery and translucent, like a pale *L. marginata*. The keel is short and inconspicuous. A pair of body bands, high up near the mid-dorsal line, are usually more or less interrupted and with scalloped outer edges. Sometimes faint traces of a second pair of bands occur lower down. A pair of mantle bands, becoming broader and darker behind, form a lyre-shaped figure, and the area enclosed is often darker in the centre and mottled with brown. The respiratory orifice is pale bordered. The tripartite sole is uniformly pale.

External variation

The mantle and body bands vary in width, completeness and the degree of crenulation of their outer borders, and there are sometimes faint traces of a second pair of body bands.

Jaw

Pale yellow, 2·25 mm across.

Radula (Text-fig. 17 D)

Like that of *Agriolimax* in having a distinctly tricuspid central tooth, and endocones on the lateral teeth—a feature which led Pollonera (1887*a* : 2) to place the species erroneously in that genus. The tri-cuspid central tooth is flanked by fifty-five to sixty teeth on each side, of which about fifteen are typical laterals with endo- and ectocones. Most of the inner marginals are simply aculeate, but many of the outer ones are bifid, while in the extreme outer ones the main cusp becomes multidenticulate.

Alimentary system

The intestine shows the two forwardly-directed loops and the long rectal caecum reaching to the apex of the visceral mass, as in *L. marginata* and *Limax flavus*.

Reproductive system (Text-fig. 17 A)

Similar to that of *L. marginata*, but with the penial appendix longer, and bluntly cylindrical rather than conical. Pollonera (1887*a*) figures the appendix of *valentianus* as dilated and terminally vesicular, but this may result from misinterpretation of a somewhat folded appendix (Simroth, 1887). Altena (1950) found that Canadian specimens had simple cylindrical appendices, like those of specimens from Swansea. Another difference from *L. marginata* is that the sac into which the spermatheca duct expands is somewhat sausage-shaped, rather than pyriform.

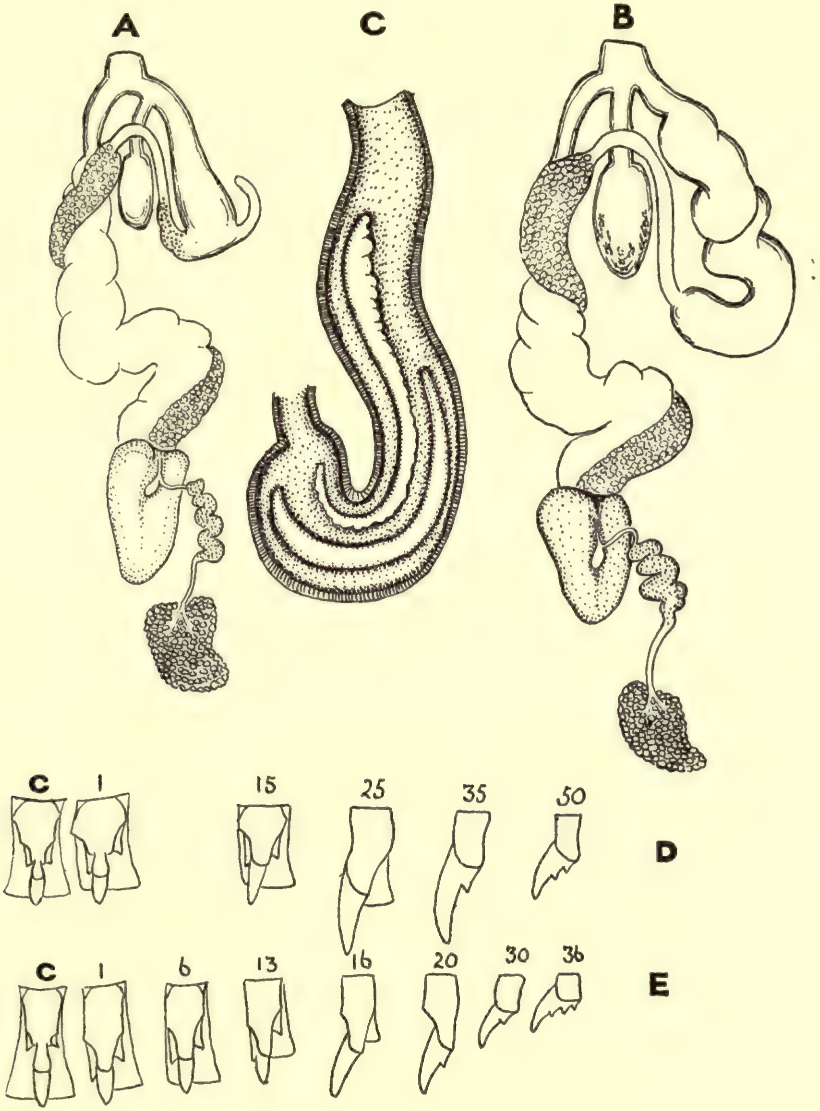


FIG. 17. Greenhouse aliens. **A.** *Lehmannia poirieri*—genital organs (× 3·3). **B.** *Limax nyctelius*—genital organs (× 3·3). **C.** *L. nyctelius*—penis (× 6·7) opened longitudinally. **D.** *L. poirieri*—representative radular teeth (× 330). **E.** *L. nyctelius*—representative radular teeth (× 330).

Mating, development

No observations on mating seem to have been recorded. Eggs laid in captivity at Swansea in December 1939 were translucent yellow and measured 2·25 × 1·5 mm. They hatched in February. In March the young measured 10·0 mm long, and had intensely black body and mantle bands, and by 10th June they were full grown.

Ecology

Found always on the ground, never climbing trees and plants like *L. marginata*. This is true in Tenerife (Altena, 1950) and California (Gregg, *in litt.*), and in a greenhouse at Swansea, where the species was always found under pots.

Distribution

Spain, the Canary Isles (? introduced), and introduced into California and Britain (known from greenhouses in Reading, Swansea and Belfast).

Material examined

Living specimens taken from a greenhouse in Singleton Park, Swansea, Glamorgan, in 1936, 1938 and 1949; and from a Reading University greenhouse at Shinfield, Reading, in 1959. Spirit specimens from Verdugo Woodlands, Glendale, California (collected by Dr. W. O. Gregg); Güejar de la Sierra, Provincia de Granada, South Spain, and Elizondon, Navarre, North Spain (collected by Dr. de Zarate) and Barcelona.

Limax nyctelius Bourguignat, 1861

Limax nyctelius Bourguignat, 1861 : 305, pl. 2, figs. 3 and 4. Algeria.

First British record

By Quick (1949 : 25). However, A. R. Waterston had found it some years before this, and partially described the species in an unpublished thesis.

Diagnostic features

Externally like *Lehmannia poirieri*, and with a similar radula. Internally resembles *L. flavus* in having a long rectal caecum, and a long cylindrical penis without an appendix.

External appearance

L. nyctelius is about 5 cm long, pale greyish-yellow with a thin translucent body-wall. There is a short inconspicuous keel at the hinder end. The mantle bands form a lyre-shaped figure, and the narrow body bands are high up on each side near the mid-dorsal line. The respiratory orifice has a pale border, and the sole is uniformly pale.

External variation

The mantle and body bands vary somewhat in breadth and intensity. Like those of *Lehmannia poirieri*, they tend to fade in alcohol.

Jaw

Dark brown or blackish, 1·7 mm across.

Radula (Text-fig. 17 E)

A tri-cuspid median tooth is flanked on each side by thirteen to fifteen tri-cuspid laterals and from twenty-eight to thirty aculeate marginals. The marginals beyond about the nineteenth are bifid, and the extreme marginals trifid.

Alimentary system

As in *L. flavus*, with two forwardly-directed loops and a long rectal caecum.

Reproductive system (Text-fig. 17 B)

The pigmented ovotestis is exposed between the right and left lobes of the liver. The pigmented hermaphrodite duct becomes swollen and folded in its central portion, and ends at the large albumen gland with a pale oval seminal vesicle. The free oviduct is short and stout. The spermatheca arises by a wide duct from the atrium, which expands abruptly to an oval sac which may be pigmented. The penis is uniformly cylindrical, more or less folded, and the vas deferens enters its apex under cover of the stout penial retractor muscle, which arises from the diaphragm close behind the kidney. Internally the penis (Text-fig. 17 C) resembles that of *L. flavus* in containing a prominent fold starting at the apex and expanding below to a " comb ", and another shorter smooth fold.

Ecology

Recorded from greenhouses and garden frames in Britain, on date palms in Washington, D.C., and beneath flower pots in Egypt (Abu Teira, *in litt.*).

Distribution

North African coast and Egypt. Introduced into Britain (known from greenhouses in Edinburgh and Glasgow), North America (known from Washington, D.C.) and South Africa (Connolly 1939 : 176).

Material examined

Spirit specimens from the Royal Botanic Gardens, Edinburgh (sent by A. R. Waterston), Shebin El Kom, Egypt, Algeria and Washington, D.C.

FOSSIL SPECIES

Limax modioliformis Sandberger, 1880

Limax modioliformis Sandberger, 1880 : 103, pl. xii, figs. 15–15 c.

Fossil shells ascribed to this species are found in the Cromerian at West Runton, Norfolk (Sandberger, 1880). However, the specific ascription of fossil slug shells is at best only tentative. Similar shells in the same beds are ascribed to *Lehmannia marginata*.

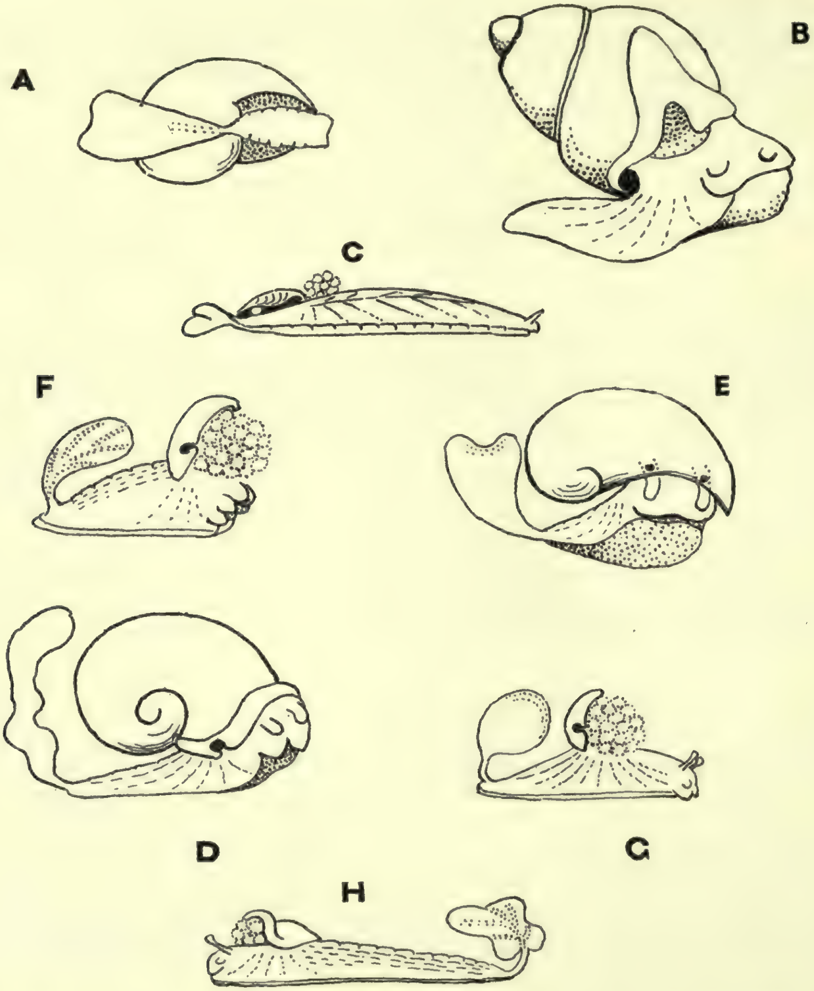


FIG. 18. Embryonic vesicles. **A.** *Achatina fulica*—embryo (× 6·7) showing large caudal vesicle. **B.** *A. fulica*—later embryo (× 6·7) with vesicle adsorbed. **C.** *Testacella scutulum*—embryo (× 6·7) showing cephalic and caudal vesicles. **D.** *Helix aspersa*—embryo (× 13) showing caudal vesicle, cephalic vesicle adsorbed. **E.** *Helicella itala*—embryo (× 20) showing caudal vesicle, cephalic vesicle adsorbed. **F.** *Arion ater*—embryo (× 17) three weeks after laying, with cephalic and caudal vesicles. **G.** *Agriolimax caruanae*—embryo (× 17) with cephalic and caudal vesicles. **H.** *Limax cinereoniger*—embryo (× 6·7) with cephalic and caudal vesicles.

ANATOMICAL TERMS

The following terms are used throughout this paper, in discussing the genital anatomy of slugs. They are illustrated by somewhat generalized illustrations in Text-fig. 19.

Ovotestis	The hermaphrodite gonad, far back in the visceral mass, producing ova and spermatozoa.
Hermaphrodite duct	The slender duct conveying ova and spermatozoa from the ovotestis to the albumen gland, oviduct and prostate.
Seminal vesicle	A loop, enlargement or diverticulum of the hermaphrodite duct at the albumen gland, for the storage of the animal's spermatozoa.
Albumen gland	A more or less linguiform gland at the termination of the hermaphrodite duct, supplying the egg albumen.
Fertilization sac	A cavity at the commencement of the oviduct where the ova are fertilized by the partner's spermatozoa.
Prostate	Glandular tubules, opening into the male duct or groove which conveys the spermatozoa.
Sperm-oviduct	The combined prostate, male duct or groove and oviduct. The prostate usually appears as a yellow ribbon on the gelatinous-looking oviduct. In the Stylommatophora, the proximal parts of the male and female tracts are not completely separate from one another.
Vas deferens	The slender male duct after it becomes separate and leaves the sperm-oviduct.
Free oviduct	The female duct, beyond the point where the vas deferens leaves it.
Spermatheca	The expanded termination of the spermatheca duct, which arises near the termination of the free oviduct (*Milax*) or directly from the atrium (*Arion*, *Limax* and *Agriolimax*). The spermatheca temporarily stores the partner's spermatozoa.
Vagina	The part of the free oviduct between the origin of the spermatheca duct and the atrium. When the spermatheca duct arises directly from the atrium, there is no vagina.
Atrium	The terminal portion of the genital ducts, receiving the oviduct, penis and often the spermatheca duct.
Epiphallus	The enlarged terminal portion of the vas deferens, which secretes the spermatophore and leads to the penis.
Spermatophore	A chitinous capsule containing a mass of spermatozoa (*Arion*, *Milax*).
Penis	The terminal evaginable portion of the male duct, leading to the atrium, and sometimes (*Milax*) containing a penial papilla.
Retractor penis muscle	A muscle arising from the body-wall and inserted between the epiphallus (when one is present) and the proximal end or apex of the penis. In *Arion* a penis and retractor are not present; the epiphallus enters the atrium direct, and a retractor muscle is inserted on the free oviduct and the spermathecal duct.
Flagellum	A slender tubular diverticulum from the apex of the penis (*Testacella*).
Penial appendix	A conical or digitiform appendage of the penis (*Lehmannia*), or a more or less branched appendage at the apex of the penis (*Agriolimax*).
Sarcobelum	A stimulatory organ situated in the penis (*Agriolimax*).
Stimulator	A stimulatory organ situated in the atrium (*Milax*).
Ligula	A lobulated or frilled mass in the atrium or lower part of the oviduct in *Arion*, which in copula functions as an adhesive organ between the partners.
Vaginal glands	A mass of glandular tubules in *Milax*, discharging into the termination of the oviduct and the atrium.

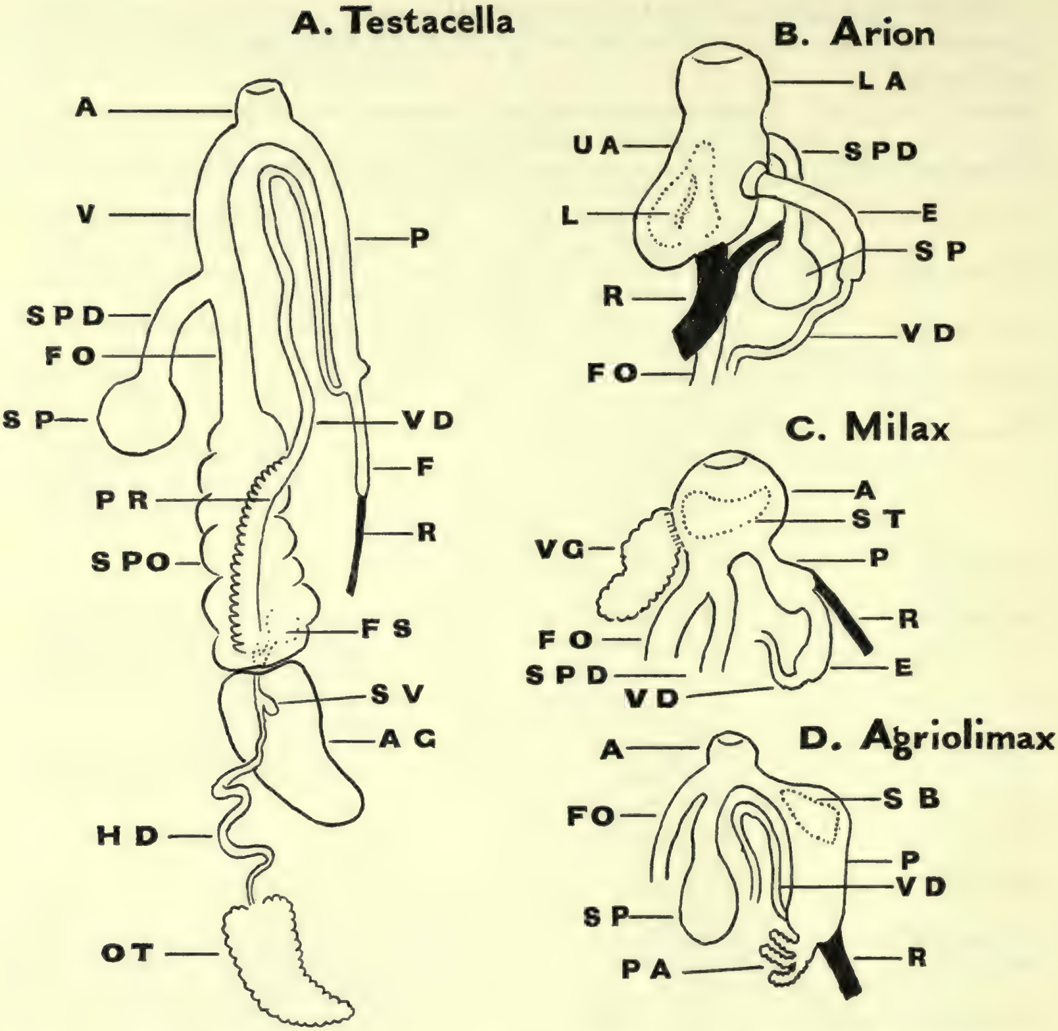
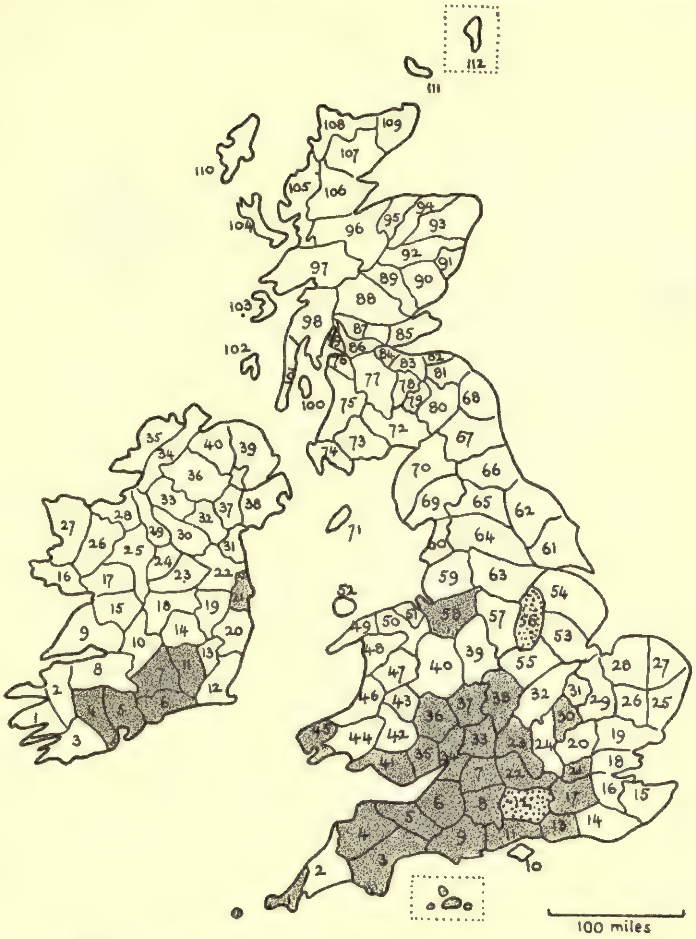

A. Testacella
A
V
P
S P D
F O
S P
V D
F
P R
R
S PO
F S
S V
A G
H D
O T
B. Arion
L A
U A
S P D
L
E
S P
R
V D
F O
C. Milax
A
S T
V G
P
R
F O
S P D
E
V D
D. Agriolimax
A
S B
F O
P
V D
S P
R
P A

FIG. 19. Genital anatomy. A. *Testacella.* B. *Arion.* C. *Milax.* D. *Agriolimax.*

Key: A—atrium
AG—albumen gland
E—epiphallus
F—flagellum
FO—free oviduct
FS—fertilization sac
HD—hermaphrodite duct
L—ligula
LA—lower atrium
OT—ovotestis
P—penis
PA—penial appendix
PR—prostate
R—retractor muscle
SB—sarcobelum
SP—spermatheca
SPD—spermatheca duct
SPO—spermoviduct
ST—stimulator
SV—seminal vesicle
UA—upper atrium
V—vagina
VD—vas deferens
VG—vaginal glands.

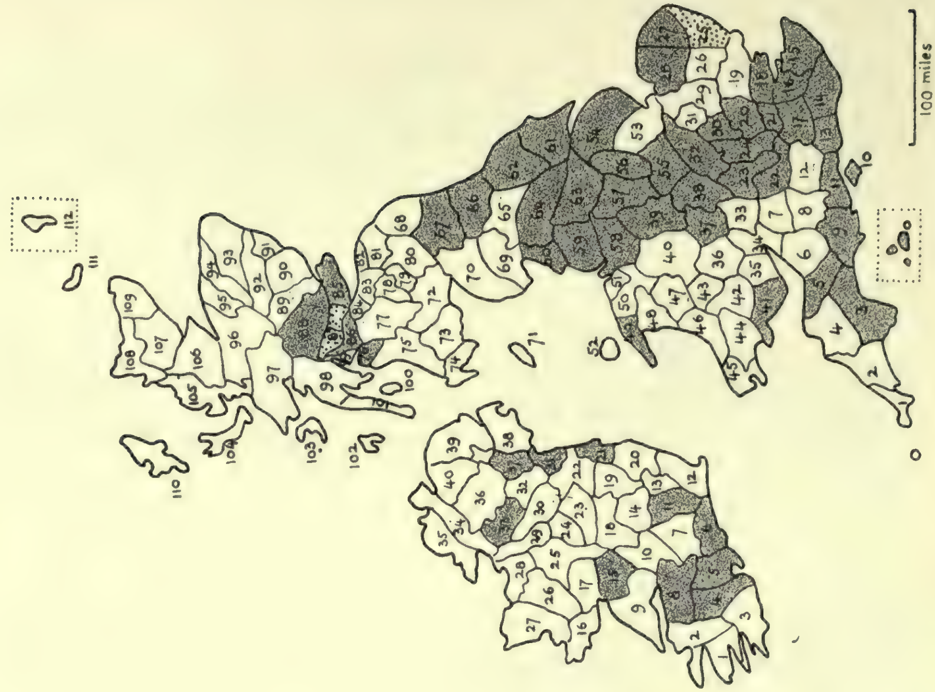
DISTRIBUTION

The numeration of vice-counties adopted in the following maps is that of Druce (1932) and the *New Naturalist* series, not that of the Conchological Society Census (Ellis, 1951). In citing vice-counties by numbers, the Irish series should be prefixed by " H ".

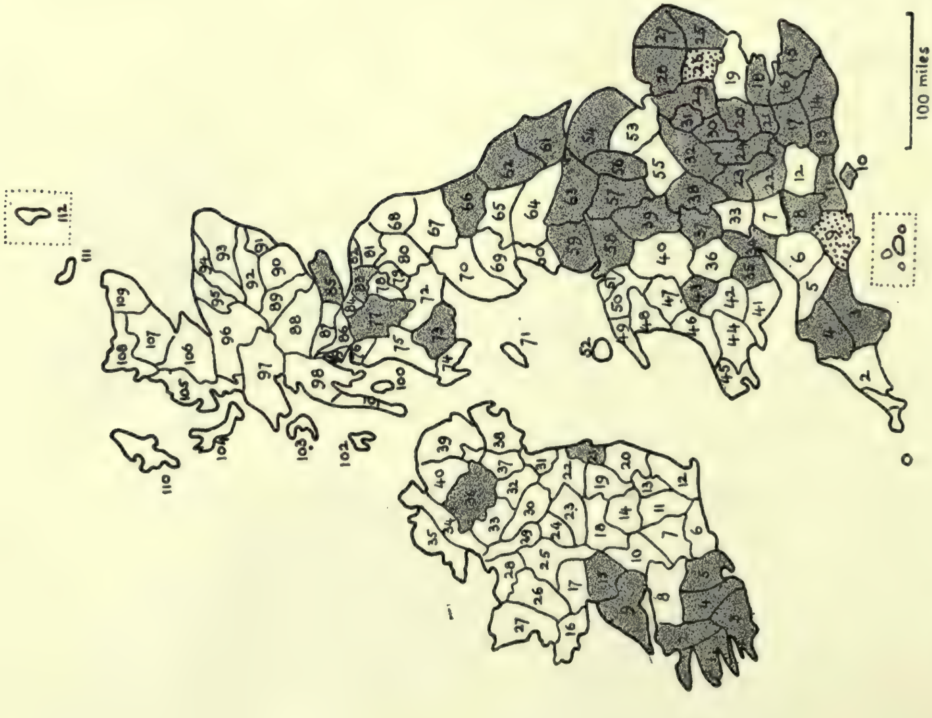


MAP 1.—Distribution of *Testacella maugei* in Britain.

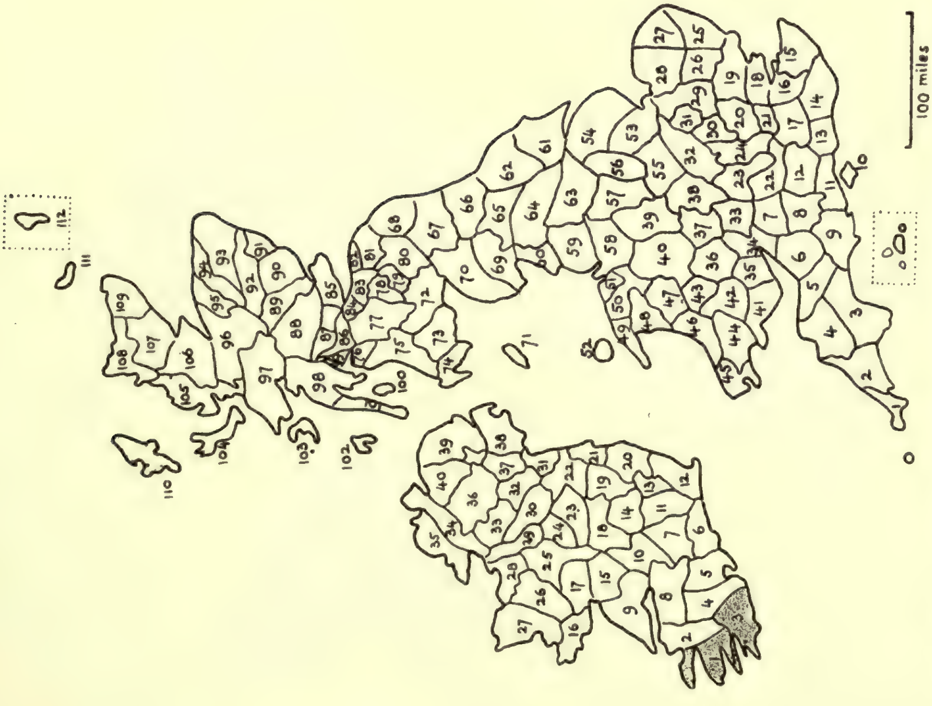
	ENGLAND AND WALES
0	Channel Isles
	PENINSULA
1	Cornwall W.
2	Cornwall E.
3	Devon S.
4	Devon N.
5	Somerset S.
6	Somerset N.
	CHANNEL
7	Wilts N.
8	Wilts S.
9	Dorset
10	Isle of Wight
11	Hants S.
12	Hants N.
13	Sussex S.
14	Sussex E.
	THAMES
15	Kent E.
16	Kent W.
17	Surrey
18	Essex S.
19	Essex N.
20	Herts
21	Middlesex
22	Berks
23	Oxford
24	Bucks
	ANGLIA
25	Suffolk E.
26	Suffolk W.
27	Norfolk E.
28	Norfolk W.
29	Cambridge
30	Bedford
31	Hunts
32	Northampton
	SEVERN
33	Gloucester E.
34	Gloucester W.
35	Monmouth
36	Hereford
37	Worcester
38	Warwick
39	Stafford
40	Salop
	SOUTH WALES
41	Glamorgan
42	Brecon
43	Radnor
44	Carmarthen
45	Pembroke
46	Cardigan
	NORTH WALES
47	Montgomery
48	Merioneth
49	Carnarvon
50	Denbigh
51	Flint
52	Anglesey
	TRENT
53	Lincoln S.
54	Lincoln N.
55	Leicester and Rutland
56	Notts
57	Derby
	MERSEY
58	Cheshire
59	Lancashire S.
60	Lancashire Mid
	HUMBER
61	S.E. York
62	N.E. York
63	S.W. York
64	Mid. W. York
65	N.W. York
	TYNE
66	Durham
67	Northumb. S.
68	Cheviotland
	LAKES
69	Westmorland and N. Lancs.
70	Cumberland
71	Isle of Man
	SCOTLAND
	W. LOWLANDS
72	Dumfries
73	Kirkcudbright
74	Wigtown
75	Ayr
76	Renfrew
77	Lanark
	E. LOWLANDS
78	Peebles
79	Selkirk
80	Roxburgh
81	Berwick
82	Haddington
83	Edinburgh
84	Linlithgow
	S. HIGHLANDS
85	Fife and Kinross
86	Stirling
87	Pth. S. and Clkn.
88	Mid. Perth
89	Perth N. (or E.)
90	Forfar
91	Kincardine
92	Aberdeen S.
	E. HIGHLANDS
93	Aberdeen N.
94	Banff
95	Elgin
96	Easterness
	W. HIGHLANDS
97	Westerness
98	Main Argyll
99	Dumbarton
100	Clyde Isles
101	Cantire
102	Ebudes S.
103	Ebudes Mid.
104	Ebudes N.
	N. HIGHLANDS
105	Ross W.
106	Ross E.
107	Sutherland E.
108	Sutherland W.
109	Caithness
	NORTH ISLES
110	Hebrides
111	Orkneys
112	Shetlands
	IRELAND
1	Kerry S.
2	Kerry N.
3	Cork W.
4	Cork Mid.
5	Cork E.
6	Waterford
7	Tipperary S.
8	Limerick
9	Clare
10	Tipperary N.
11	Kilkenny
12	Wexford
13	Carlow
14	Queen's Co.
15	Galway S. E.
16	Galway W.
17	Galway N.E.
18	King's Co.
19	Kildare
20	Wicklow
21	Dublin
22	Meath
23	Westmeath
24	Longford
25	Roscommon
26	Mayo E.
27	Mayo W.
28	Sligo
29	Leitrim
30	Cavan
31	Louth
32	Monaghan
33	Fermanagh
34	Donegal E. (or S.)
35	Donegal W. (or N.)
36	Tyrone
37	Armagh
38	Down
39	Antrim
40	Derry



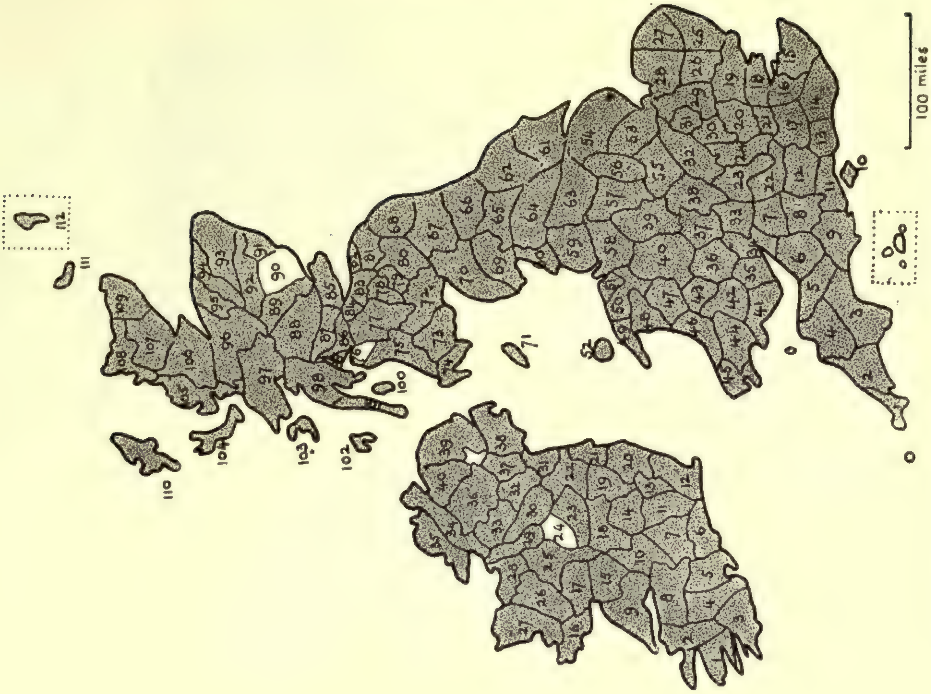
MAP 3.—Distribution of *Testacella scutulum* in Britain.



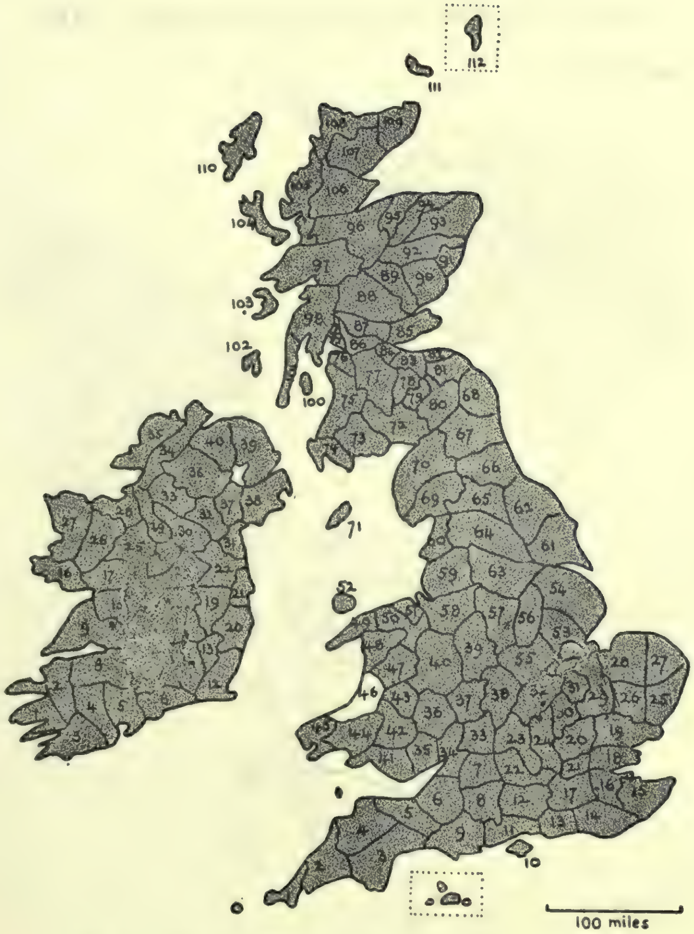
MAP 2.—Distribution of *Testacella haliotidea* in Britain.



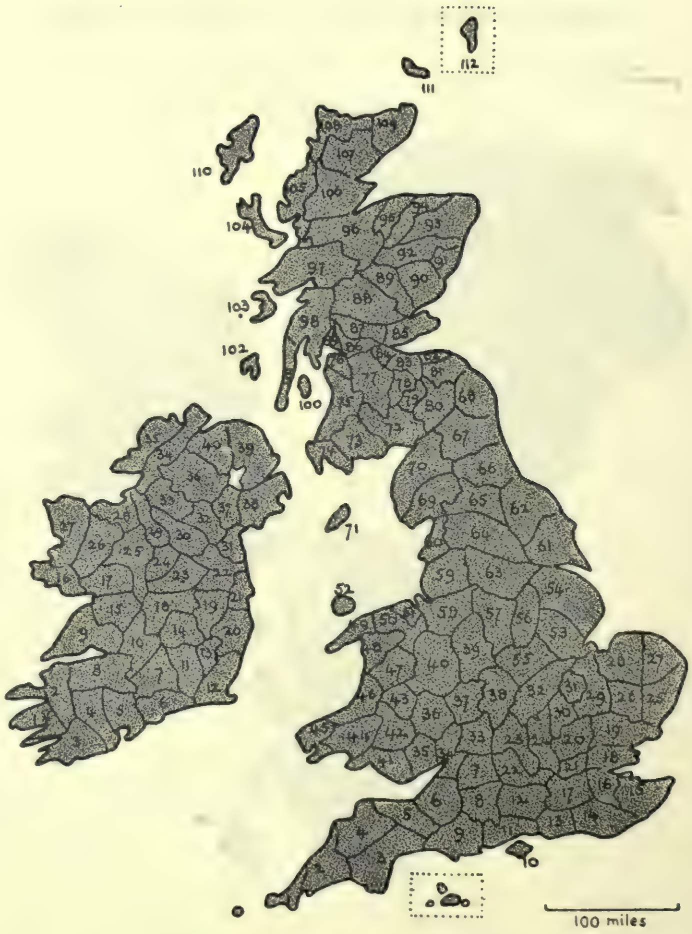
MAP 4.—Distribution of *Geomalacus maculosus* in Britain.



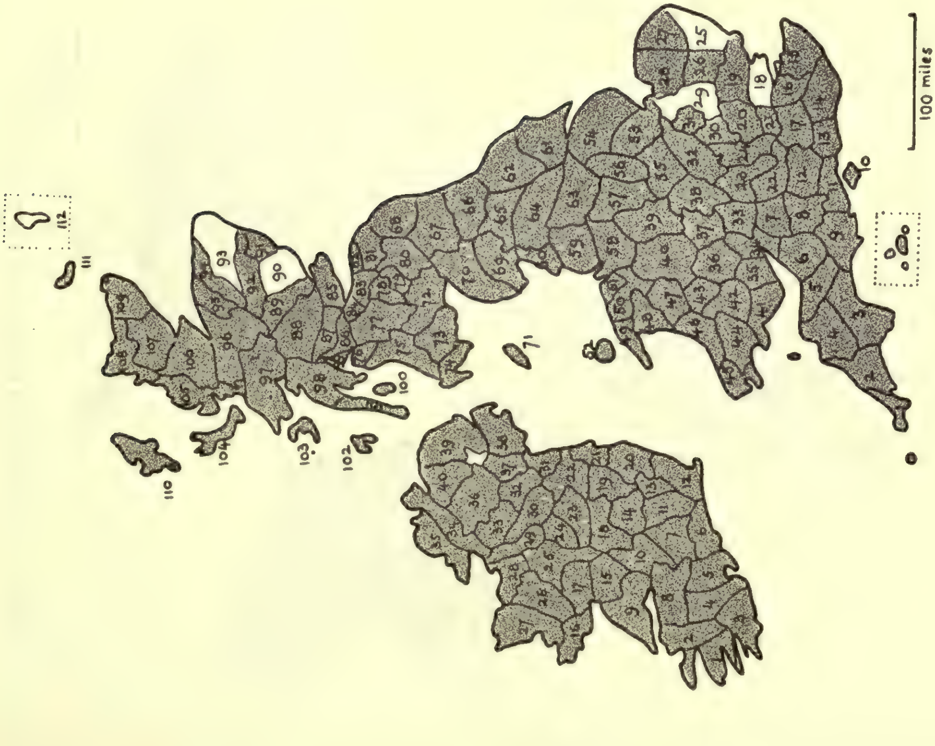
MAP 5.—Distribution of *Arion intermedius* in Britain.



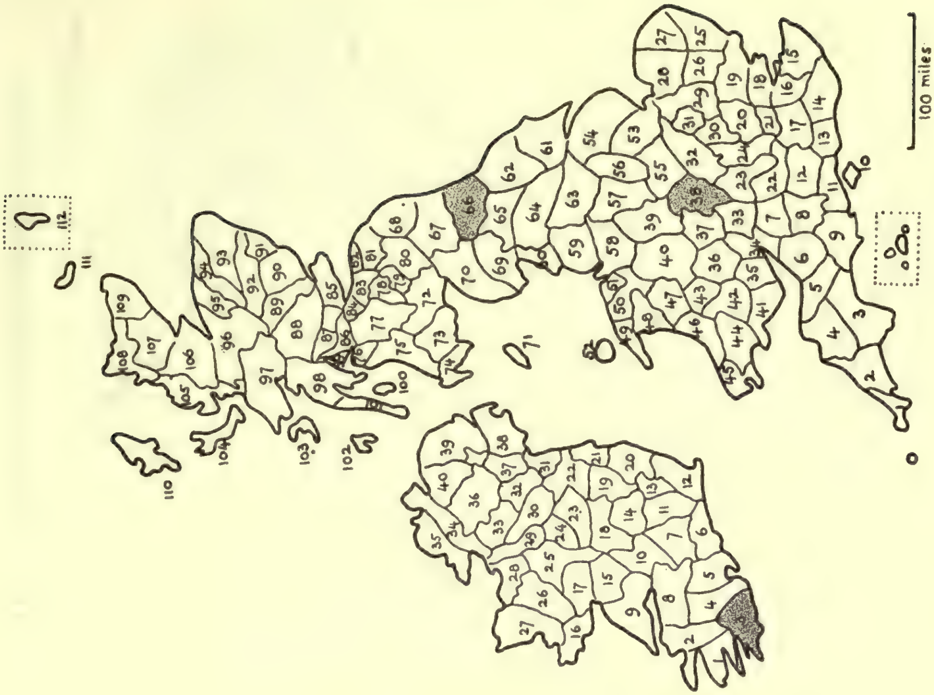
Map 6.—Distribution of *Arion fasciatus* in Britain.



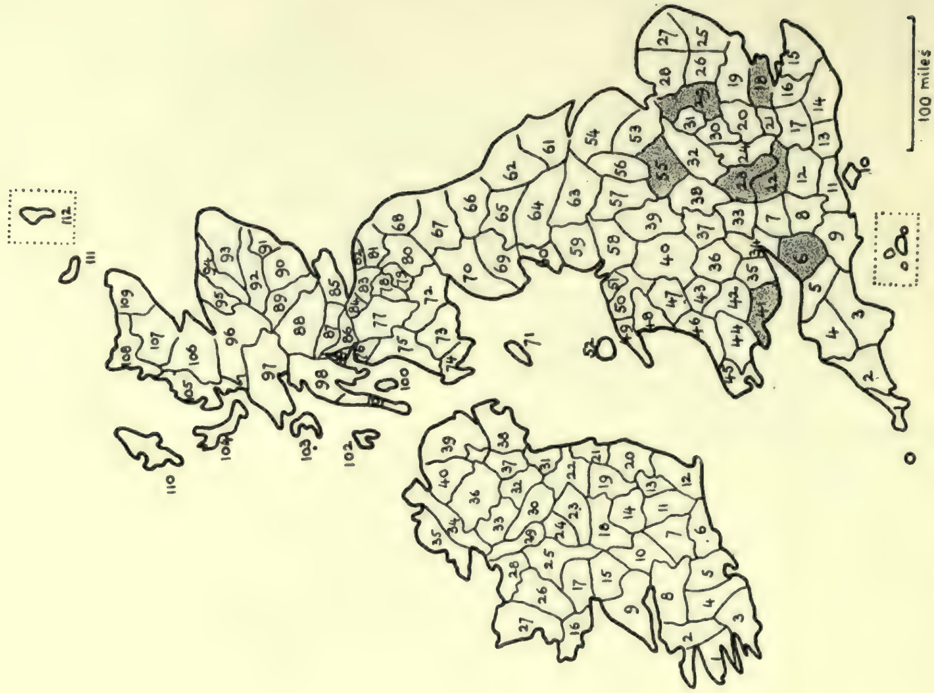
Map 7.—Distribution of *Arion hortensis* in Britain.



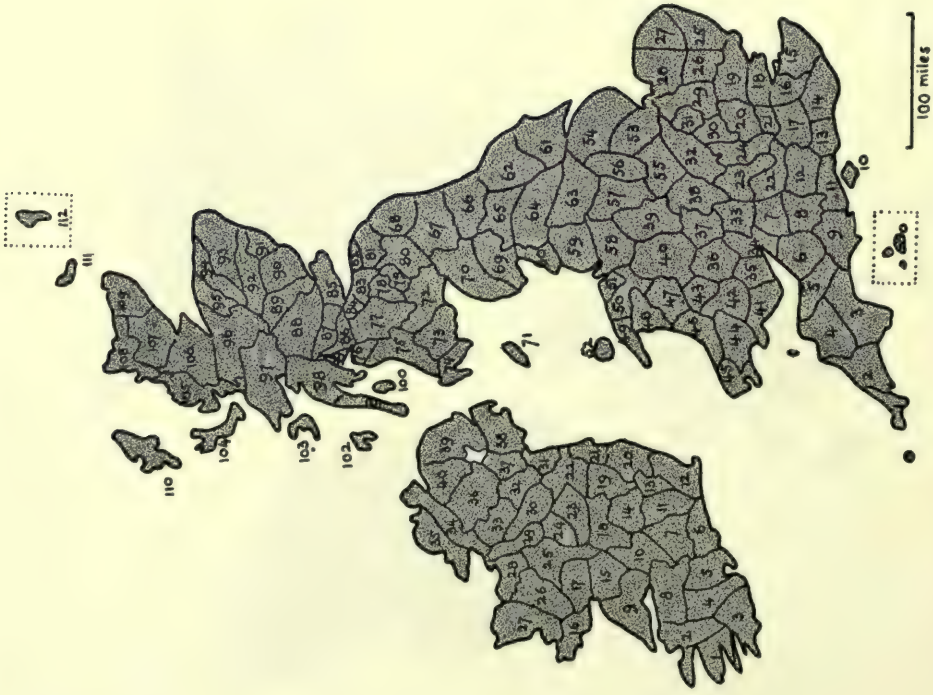
MAP 8.—Distribution of *Arion subfuscus* in Britain.



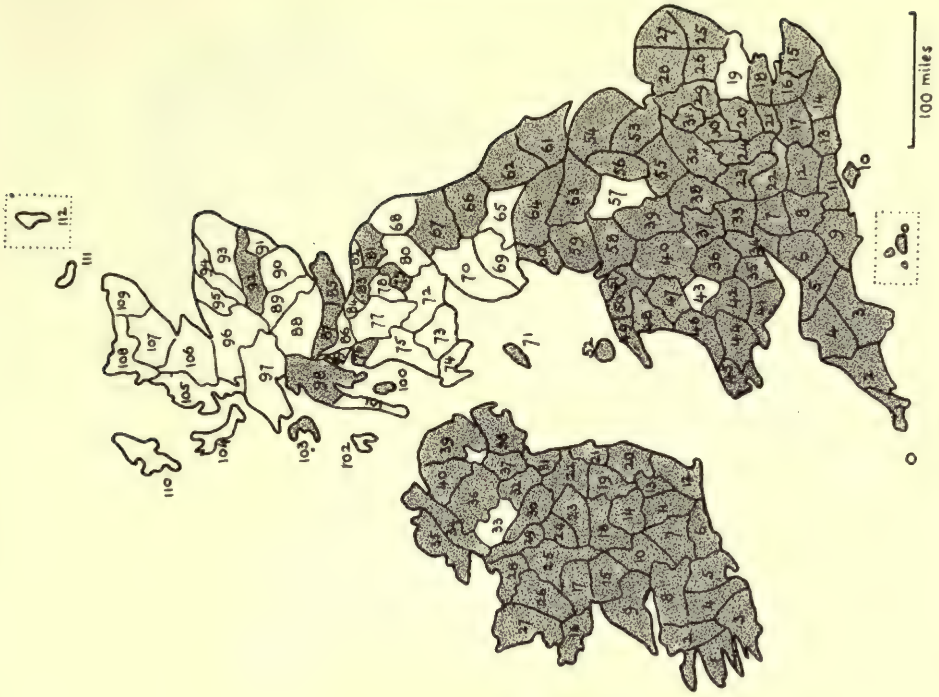
MAP. 9—Distribution of *Arion lusitanicus* in Britain.



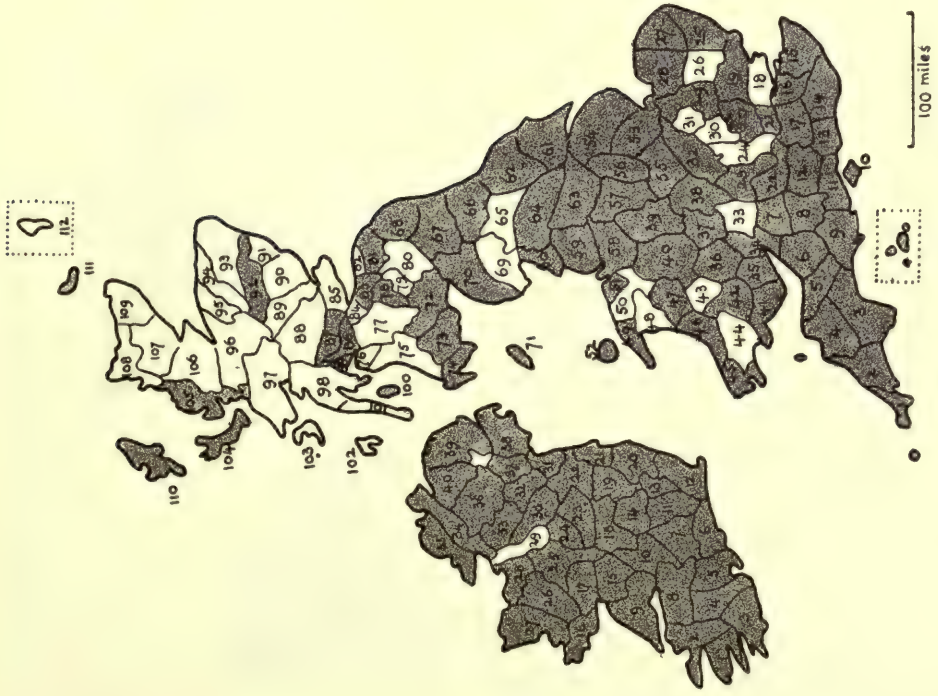
MAP 11.—Distribution of *Arion ater rufus* in Britain.



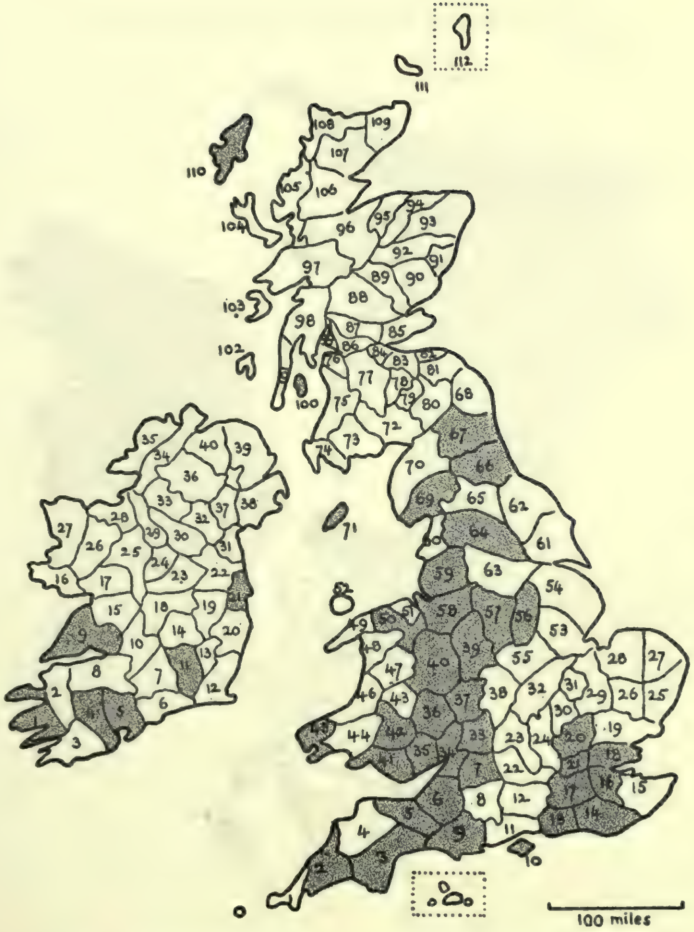
MAP 10.—Distribution of *Arion ater ater* in Britain.



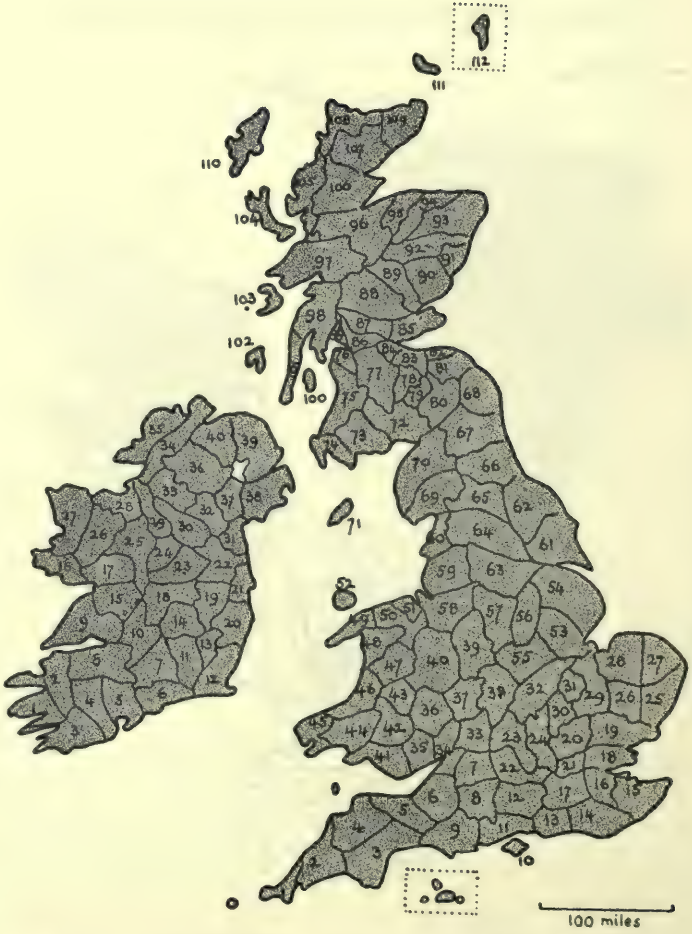
MAP 13.—Distribution of *Milax sowerbyi* in Britain.



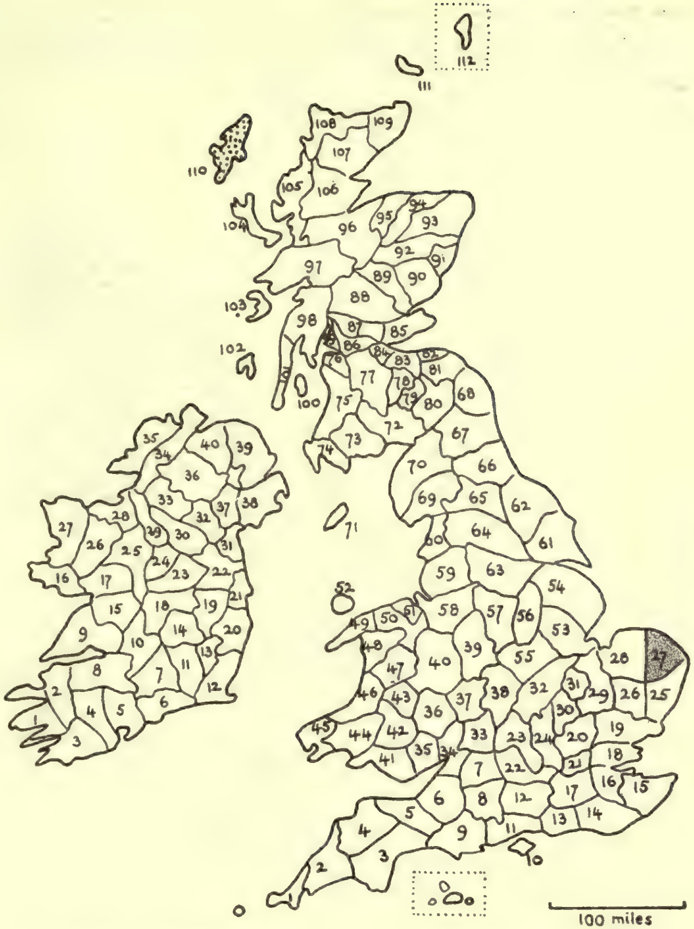
MAP 12.—Distribution of *Milax gagates* in Britain.



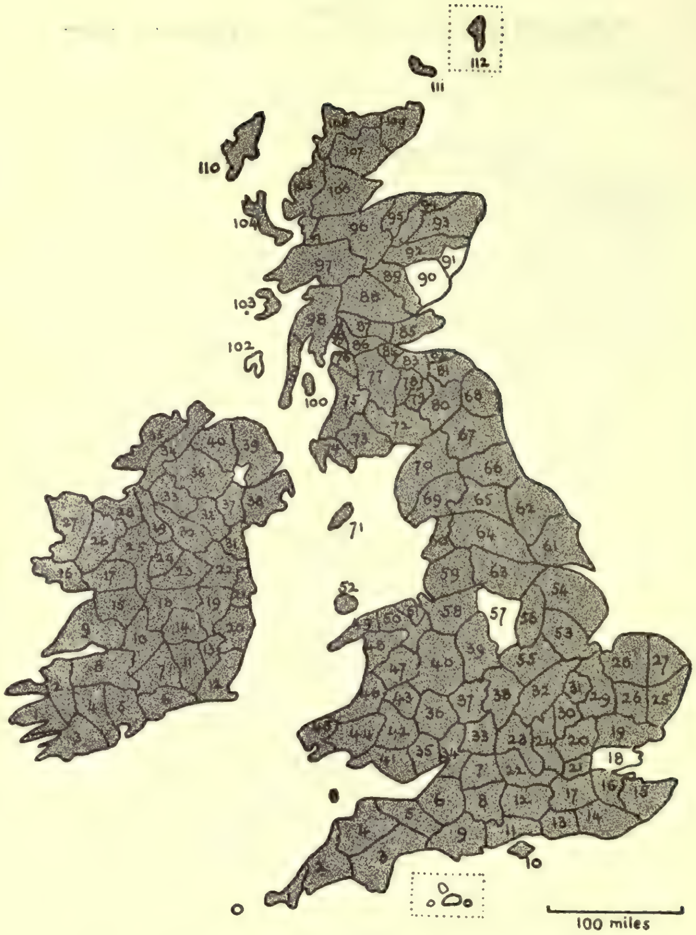
Map 14.—Distribution of *Milax budapestensis* in Britain.



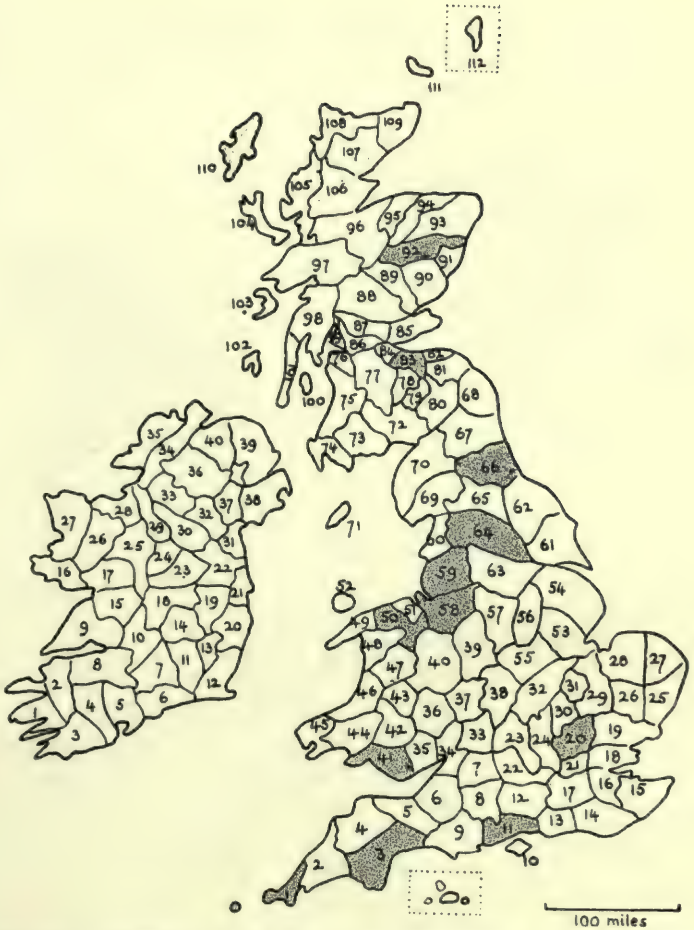
Map 15.—Distribution of *Agriolimax reticulatus* in Britain.



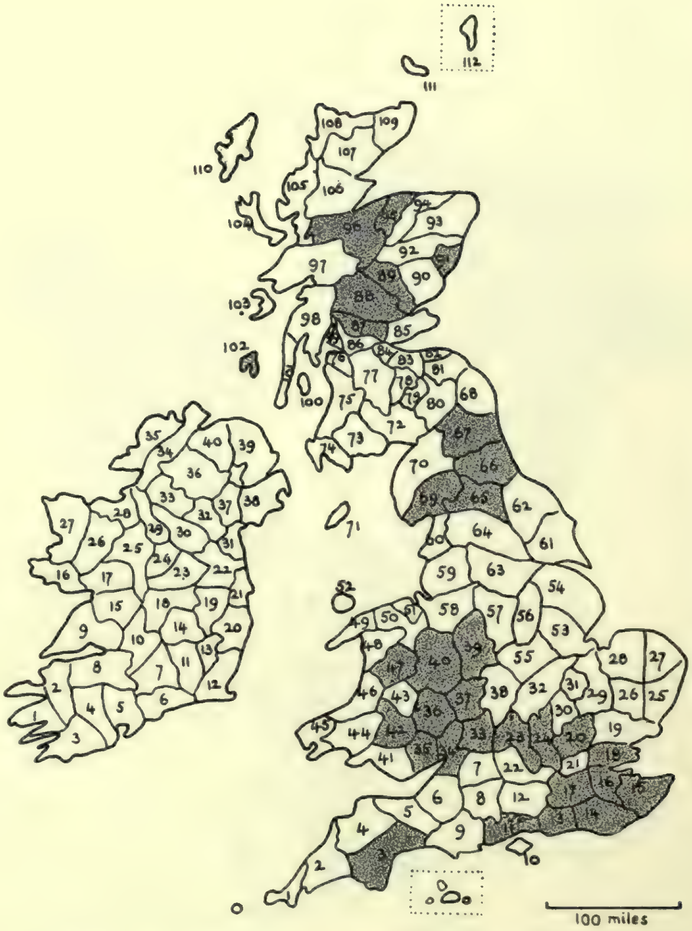
MAP 16.—Distribution of *Agriolimax agrestis* in Britain.



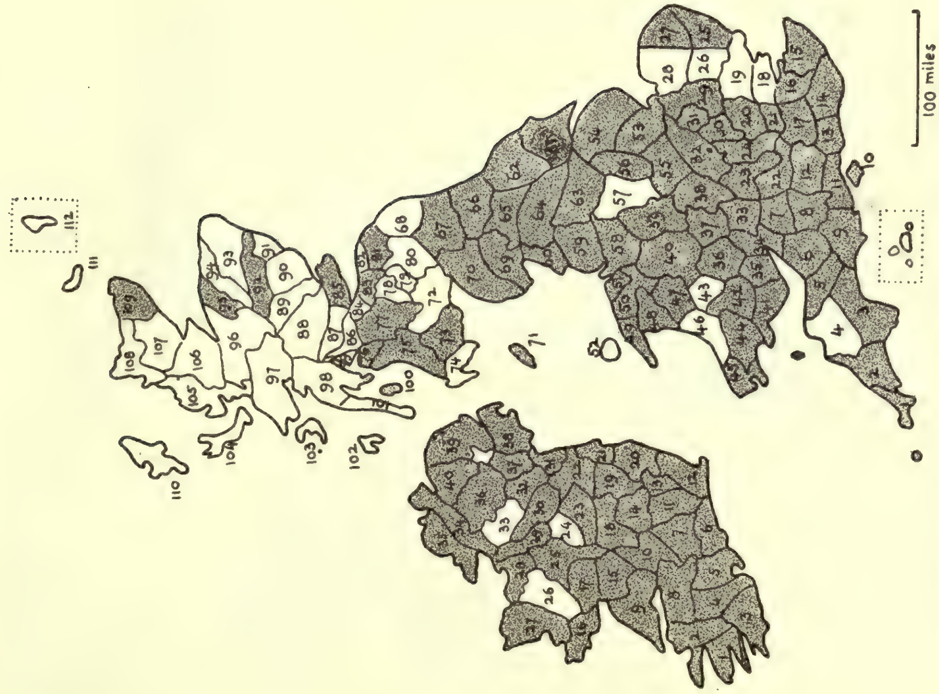
MAP 17.—Distribution of *Agriolimax laevis* in Britain.



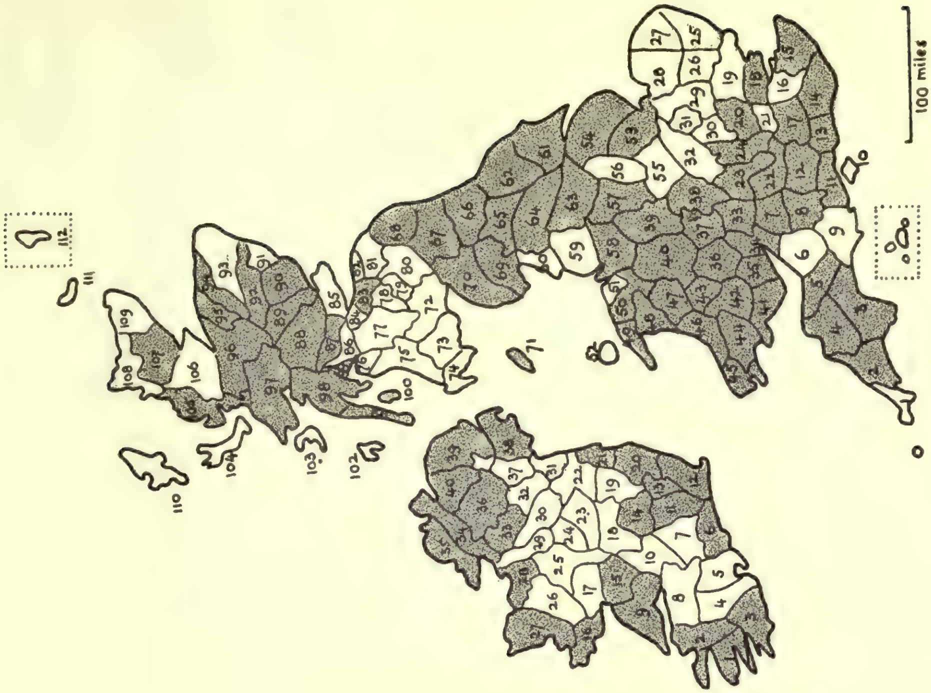
MAP 18.—Distritution of *Agriolimax caruanae* in Britain. New records from Ireland need to be added: Cork Mid. (H4) and Down (H38).



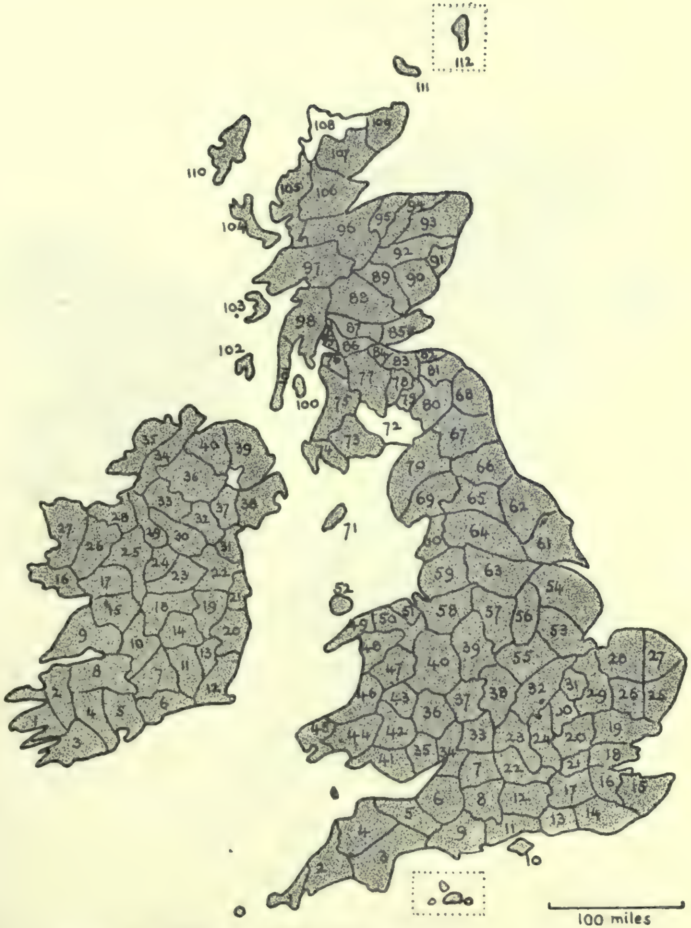
MAP. 19.—Distribution of *Limax tenellus* in Britain.



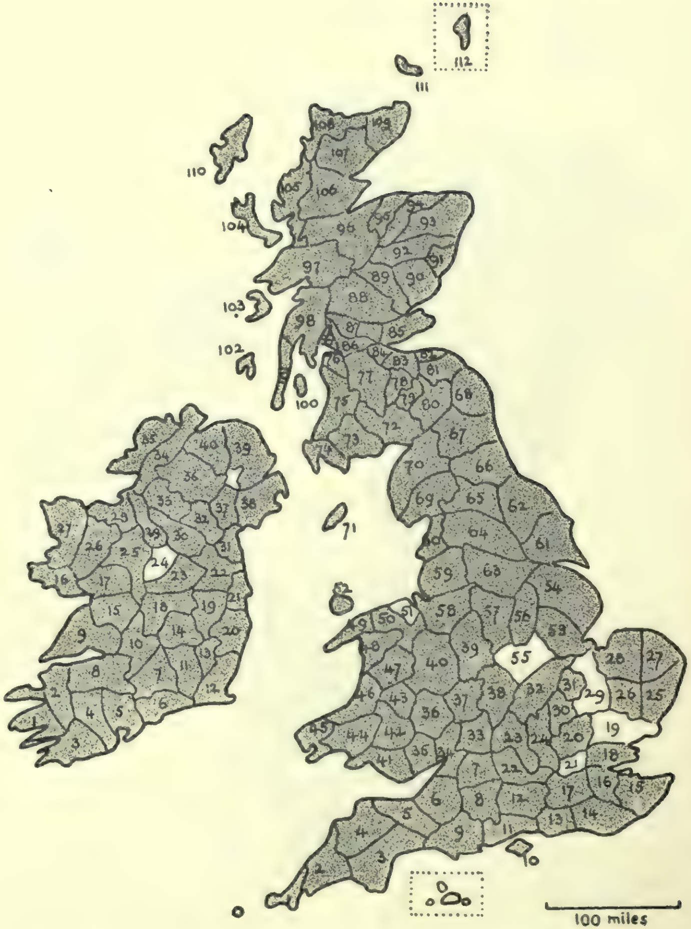
Map. 20.—Distribution of *Limax flavus* in Britain.



Map. 21.—Distribution of *Limax cinereoniger* in Britain.



MAP 22.—Distribution of *Limax maximus* in Britain.



MAP 23.—Distribution of *Lehmannia marginata* in Britain.

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PLATE 1

The scale lines represent one centimetre.

1. *Geomalacus maculosus.*
2. *Arion subfuscus.*
3. *Arion ater ater.*
4. *Arion hortensis.*
5. *Arion fasciatus.*
6. *Arion intermedius.*
7. *Arion intermedius* (contracted).
8. *Arion fasciatus* (contracted).
9. *Arion subfuscus* (young).
10. *Testacella haliotidea.*
11. *Arion ater rufus* (young).
12. *Milax gagates* (contracted).
13 *Testacella maugei.*
14. *Lehmannia poirieri.*

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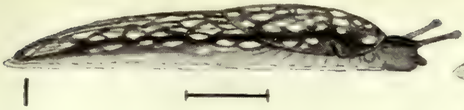
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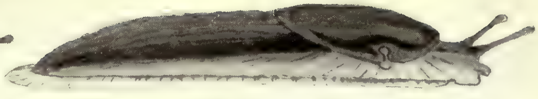
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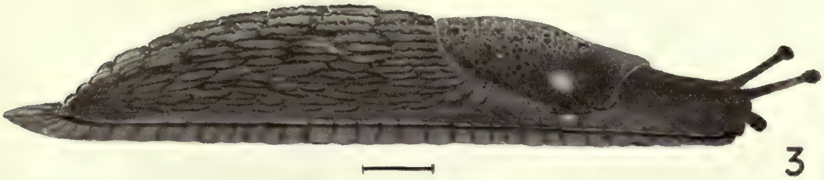
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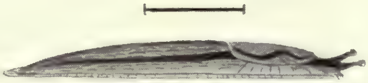
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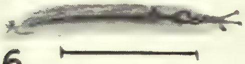
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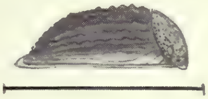
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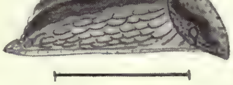
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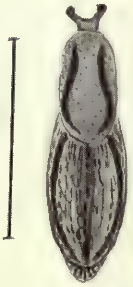
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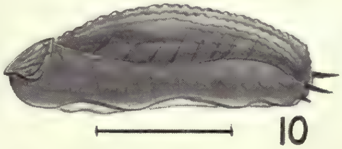
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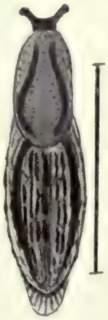
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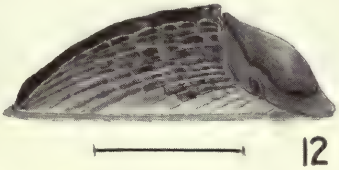
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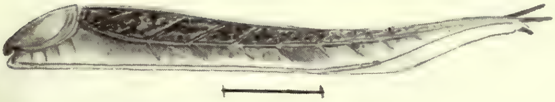
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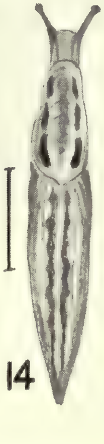
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PLATE 2

The scale lines represent one centimetre.

15. *Agriolimax reticulatus.*
16. *Limax tenellus.*
17. *Agriolimax caruanae.*
18. *Lehmannia marginata.*
19. *Agriolimax laevis.*
20. *Milax budapestensis.*
21. *Lehmannia marginata* var. *tigrina.*
22. *Limax flavus.*
23. *Milax sowerbyi.* (contracted).
24. *Limax maximus.*
25. *Limax cinereoniger.*

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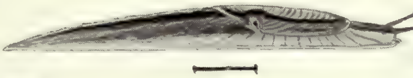

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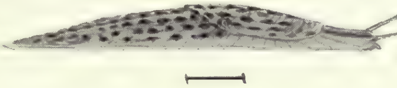

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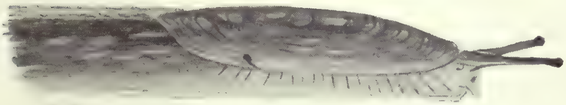

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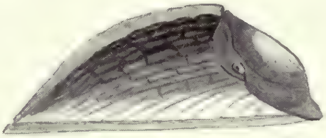

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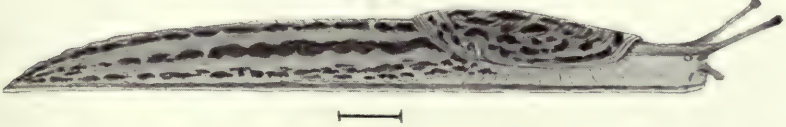

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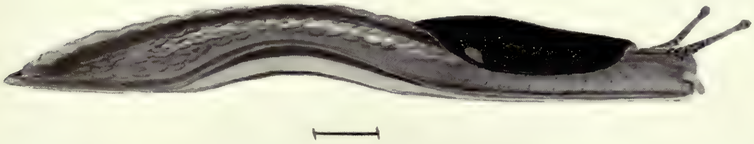

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A REVISION OF THE LAKE VICTORIA *HAPLOCHROMIS* SPECIES (PISCES, CICHLIDAE)

PART IV

BRITISH MUSEUM
13 MAR 1960
NATURAL HISTORY

P. [illegible] GREENWOOD

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 6 No. 4
LONDON : 1960

A REVISION OF THE LAKE VICTORIA *HAPLOCHROMIS* SPECIES (PISCES, CICHLIDAE)
PART IV

BY

P. H. GREENWOOD

Department of Zoology, British Museum (Natural History)

BRITISH MUSEUM
18 AUG 1960
NATURAL HISTORY

Pp. 227–281 ; 21 *Text-figures*

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A REVISION OF THE LAKE VICTORIA *HAPLOCHROMIS* SPECIES (PISCES, CICHLIDAE)
PART IV

By P. H. GREENWOOD
Department of Zoology, British Museum (Natural History)

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INTRODUCTION

IN previous parts of this series I have revised species-groups possessing common or related structural peculiarities and, in most cases, similar feeding habits. The present paper deals with a greater variety of structural and trophic types and many of the species show no obvious relationship to one another. With one exception, the species described below fall into three groups, namely, structurally generalized insectivorous species, specialized mollusc-eaters and species showing various degrees of structural and adaptational intermediacy between the other two groups. The exceptional fish, *Haplochromis martini* is a piscivorous predator ; it is included simply because of its overall resemblance to one of the insectivorous species described here.

Formerly, some of the generalized species reviewed in this paper were synonymized with one of the mollusc-eaters (*H. ishmaeli*) ; the others are included because of various resemblances to species now resurrected and redefined. One such is *Haplochromis cinereus*, a species previously considered to be the extant representative of the ancestral type from which at least part of the present flock had evolved. These views on the central evolutionary position of *H. cinereus* are no longer tenable since the " species " thought to be *H. cinereus* was a complex of several distinct species, some more generalized than the others. *Haplochromis cinereus, sensu stricto* is, in fact, an anatomically somewhat specialized derivative from an even more generalized form.

The most outstanding structural character in many of the species described below is an increase in the strength and size of the pharyngeal bones and musculature. As might be expected, these changes are reflected in the diet of the species, which usually include Mollusca as an important element in their food. Two species, *H. ishmaeli* and *H. pharyngomylus*, feed almost entirely on snails and bivalves.

Those species with the pharyngeal mill in an intermediate stage of hypertrophy are able to deal with small molluscs and also with the tubicolous larvae of certain Trichoptera, an otherwise infrequent element in the food of insectivorous *Haplochromis* without strengthened pharyngeals.

By crushing their molluscan prey within the pharynx these species stand in sharp contradistinction to the other groups of mollusc-eating *Haplochromis* in Lake Victoria. Species in this latter group remove the snail from its shell by holding the foot between the jaws and then levering the soft parts free before ingestion takes place (Greenwood, 1956*a* and 1957).

Haplochromis lacrimosus (Blgr.) 1906

(Text-fig. 1)

Tilapia lacrimosa (part) Boulenger, 1906, *Ann. Mag. nat. Hist.* (7) **17**, 450 ; *Idem*, 1907, *Fish. Nile*, 515 ; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 234, fig. 154.
Haplochromis cinereus (part) Regan, 1922, *Proc. zool. Soc. London*, 166.

Lectotype. An adult male 76 mm. standard length (B.M. [N.H.] 1906.5.30.471) from Entebbe.

Description, based on 36 specimens (including the lectotype and 10 paratypes) 66·0–97·0 mm. S.L.

Depth of body 31·8–38·7 (M = 35·5) per cent of standard length, length of head 30·8–35·5 (M = 33·5) per cent. Dorsal head profile straight or slightly curved, sloping moderately steeply. Preorbital depth 13·6–18·0 (M = 15·5) per cent of head length, showing weak positive allometry with standard length ; least interorbital width 20·8–26·9 (M = 23·5), snout length 26·6–32·2 (M = 29·6) per cent. Diameter of eye 26·1–32·6 (M = 30·4) per cent of head, ratio of eye diameter to preorbital depth 1·5–2·3 (mode 2·0) ; depth of cheek 17·6–23·5 (M = 20·8) per cent. Caudal peduncle 15·0–19·2 (M = 17·2) per cent of standard length, 1·2–1·8 (mode 1·5) times as long as deep.

Mouth horizontal or almost so ; jaws equal anteriorly, the lower 31·4–41·3 (M = 37·1) per cent of head and 1·2–2·0 (mode 1·6) times as long as broad. Posterior tip of the maxilla extending to the vertical to the anterior orbital margin or slightly beyond, rarely not quite reaching the anterior orbital margin.

Gill rakers variable, from moderately stout to slender ; 7–9 (mode 8), rarely 6 on the lower part of the first gill arch, the lowermost two or three reduced.

Scales ctenoid; lateral line with 31 (f.5), 32 (f.21) or 33 (f.8) scales; cheek with 2 or 3 (rarely 4) series; 6 or 7 (rarely $5\frac{1}{2}$) between the lateral line and the dorsal fin origin, 7 or 8 (rarely 6) between the pectoral and pelvic fin bases. Scales of the pectoral region small or moderate.

Fins. Dorsal with 24 (f.19) or 25 (f.16) rays, anal with 11 (f.19), 12 (f.16) or 13 (f.1), comprising XV–XVI, 8–10 and III, 8–10 spinous and branched rays for the fins respectively. Pectoral 82·5–100·0 (M = 88·5) per cent of head. Caudal truncate or subtruncate.

Teeth. The outer row in both jaws is composed of unequally bicuspid, relatively slender and sometimes slightly recurved teeth. Rarely, a few unicuspid teeth may occur anteriorly in this row; likewise a few posterolateral teeth in the upper jaw may be unicuspid. There are 40–60 (mode 54, modal range 48–54) teeth in the upper jaw.

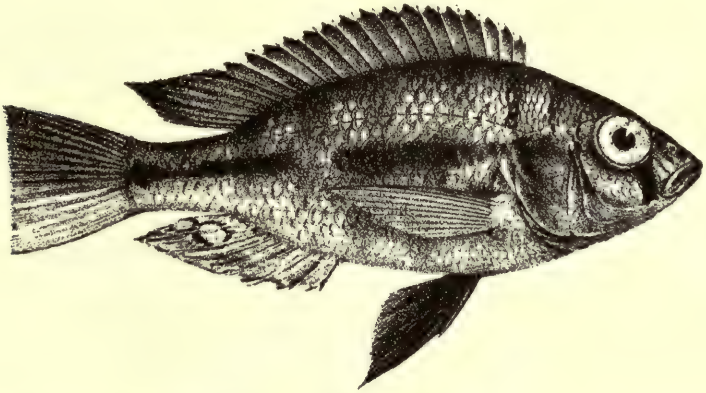

FIG. 1. *Haplochromis lacrimosus*; lectotype (from Boulenger, *Fishes of the Nile*).

Teeth in the inner series are tricuspid and implanted at a slight, posteriorly directed angle (cf. *H. cinereus* where the inner teeth lie almost horizontally); there are 2 or 3 (rarely 4) rows of inner teeth in the upper jaw and 2 (less commonly 3, rarely 4) in the lower.

Lower pharyngeal bone triangular and slender; a few slightly enlarged but bicuspid teeth may occur in the median tooth-rows.

Coloration. The colours of live fishes are unknown.

Preserved material: Sexually active males. Ground colour yellowish-silver, chest dusky; a dark lachrymal stripe is always present and in some specimens it may extend obliquely upwards through the eye and on to the nape; there are usually two transverse bands across the snout.

Two common patterns of body markings are known. (i) A large mid-lateral blotch situated slightly posterior to the pelvic fin insertion and a mid-lateral stripe running from a point above the second anal ray on to the caudal fin ; a faint transverse bar is visible immediately posterior to the edge of the operculum and two others lie between the mid-lateral blotch and the origin of the posterior stripe. The blotch itself appears to be the intensified mid-portion of a vertical bar.

(ii) Nine, close-set and ventrally ill-defined transverse bars on the flanks ; ventrally, the bars tend to run into one another so that the lower region of the flank is steely-grey.

All fins, except the pelvics, hyaline, the upper part of the caudal sometimes weakly maculate, the mid-part dark ; anal with two or three ocelli ; pelvic fins black.

Females and quiescent males. Ground colour greyish-silver, brownish above. Seven to nine faint transverse bars on the flanks, not reaching the ventral or dorsal outlines of the body. All fins hyaline.

Distribution. At present, *H. lacrimosus* is known with certainty from Lake Victoria ; Pappenheim & Boulenger (1914) recorded a specimen from Lake Edward, but I have not been able to examine their material.

Ecology : Habitat. No precise details are available for fishes already in the collections of the B.M. (Nat. Hist.) ; specimens collected by E.A.F.R.O. come from only two localities, both exposed, sandy beaches with the water depth less than 20 feet. Thus, it is impossible to generalize on the habitat preferences of *H. lacrimosus.*

Food. The stomach and intestinal contents of twenty fishes were examined ; with one exception (a fish from Entebbe) these specimens were caught at one time and at a single locality (Majita, Tanganyika Territory). The gut contents of the sixteen specimens containing food were varied. Twelve fishes contained fine sand-grains, bottom detritus (including fragments of plant epidermis and diatom frustules) and some Cladocera ; five contained remains of insect larvae (probably Diptera), one an adult dipteran, one the remains of a larval *Povilla adusta* Navás (Ephemeroptera) and one an insect egg-mass. Two fishes yielded, besides insect fragments, the remains of an oligochaet worm, whilst two others each contained the foot and soft parts of a snail. From these scanty and topographically restricted data, *H. lacrimosus* should perhaps be classified as a bottom-feeding omnivore.

Breeding. The breeding habits are unknown. Two of the smallest fishes (male and female, both 66·0 mm. S.L.) are adult. It seems possible that adult males reach a larger maximum size than do females.

Affinities. Haplochromis lacrimosus is one of the structurally and ecologically generalized species of Lake Victoria. Its most striking and apparently diagnostic character is the markings of male fishes ; but, it must be stressed that coloration is known only from preserved material. In general appearance *H. lacrimosus* resembles *H. pallidus* (see p. 233) but the two species differ in several characters besides male coloration.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.)—1906.5.30.471 (Lectotype *Tilapia lacrimosa*)	Entebbe	Degen
B.M. (N.H.)—1906.5.30.472–478	,,	,,
,, 1906.5.30.483–484	Bunjako	,,
,, 1906.5.30.488–489	Buganga	,,
,, 1907.5.7.81–82	Buddu Coast	Simon
,, 1908.10.19.2–5	Sesse Islands	Bayon
,, 1959.4.28.24	Entebbe Harbour	E.A.F.R.O.
	Tanganyika	
,, 1959.4.28.1–23	Majita	,,

Haplochromis pallidus (Blgr.) 1911

(Text-figs. 2 and 3)

Tilapia pallida (part) Boulenger, 1911, *Ann. Mus. Genova* (3), **5**, 74; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 231–2.

Labrochromis pallidus Regan, 1920, *Ann. Mag. nat. Hist.* (9), **5**, 45 (footnote).

Haplochromis cinereus (part), Regan, 1922, *Proc. zool. Soc. London*, 166.

This synonymy is tentative, as I have been unable to locate three specimens of *T. pallida* which Regan (1922) referred to *Haplochromis guiarti* (Pellegrin). Regan's genus *Labrochromis*, based on a skeleton wrongly identified as *T. pallida*, is discussed on page 275.

Description, based on twenty specimens (including the holotype and four paratypes) 43–74 mm. S.L.

Depth of body 33·3–38·8 (M = 35·4) per cent of standard length, length of head 32·3–35·3 (M = 34·1) per cent. Dorsal head profile straight or slightly curved, sloping at about 30°–40°. Preorbital depth 13·2–18·2 (M = 16·5) per cent of head; least interorbital width 21·0–30·0 (M = 24·7) per cent. Snout as long as broad or slightly longer; its length 29·1–33·4 (M = 31·2) per cent of head; diameter of eye 26·1–33·4 (M = 29·5) per cent, ratio of eye diameter to preorbital depth 1·5–2·3 (mode 1·7); depth of cheek 19·0–25·0 (M = 21·7) per cent of head. Caudal peduncle 14·2–18·5 (M = 16·2) per cent of standard length, 1·2–1·7 (mode 1·2) times as long as deep.

Mouth horizontal; jaws equal anteriorly, the lower 32·2–40·9 (M = 37·6) per cent of head and 1·4–1·8 (mode 1·6) times as long as broad. Posterior tip of the maxilla extending to the vertical through the anterior orbital margin or slightly beyond.

Gill rakers short and stout (slender in one specimen), 7–9 (mode 9), rarely 10, on the lower part of the first arch, the lowermost 1–4 (or even 5) rakers greatly reduced.

Scales ctenoid; lateral line with 31 (f.6), 32 (f.13) or 33 (f.1) scales; cheek with 2 or 3 (rarely 4) series; 6 or 7 (occasionally 5) between the lateral line and the dorsal fin origin, 6 or 7 (occasionally 8) between the pectoral and pelvic fin bases. Scales on the chest rather small.

Fins. Dorsal with 24 (f.5) or 25 (f.15) rays, anal with 11 (f.3) or 12 (f.17), comprising XV–XVI, 8–10 and III, 8 or 9 spinous and branched rays for the fins respectively. Caudal truncate ; pectoral fin 78·0–87·0 (M = 81·0) per cent of head.

Teeth. The outer row in both jaws is composed of unequally bicuspid, moderately stout teeth implanted erectly. In most fishes more than 67 mm. S.L. some unicuspid teeth occur postero-laterally in the upper jaw. The holotype (the largest specimen examined) has only weakly bicuspid teeth in the outer row. Three small specimens from near the Ripon Falls have somewhat more slender outer teeth than other specimens. There are 36–48 teeth in the upper outer series ; no clear-cut mode can be determined from the sample studied.

The small and tricuspid inner teeth are implanted at a very slight angle and arranged in 3 (rarely 2) rows in the upper jaw and 2 or 3 rows in the lower.

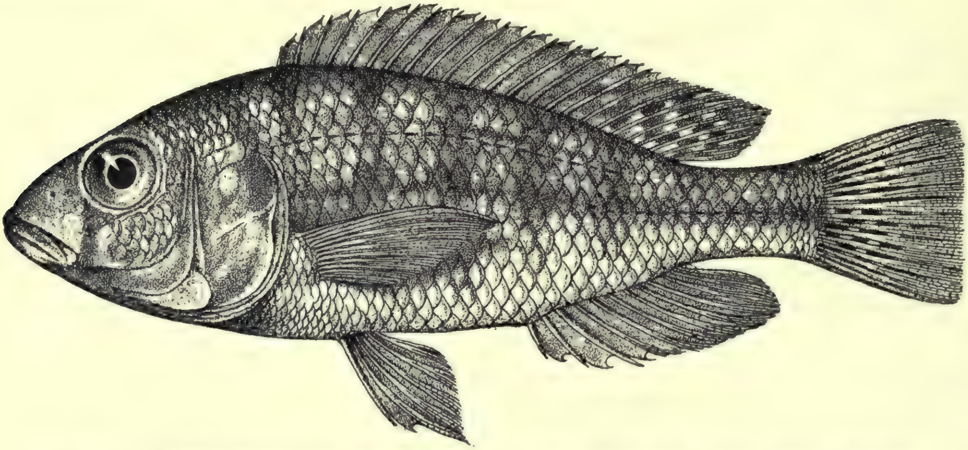

FIG. 2. *Haplochromis pallidus ;* holotype (from Boulenger, *Ann. Mus. Genova*).

Lower pharyngeal bone triangular, usually slender but slightly thickened in three specimens. Most fishes have the two median rows of teeth slightly enlarged (especially the most posterior one or two pairs) ; in a few, all the pharyngeal teeth are slender.

Coloration. The colours of live fishes are unknown.

Preserved material. Adult males. Ground colour greyish, with faint traces of up to seven dark transverse bars on the flank and caudal peduncle ; branchiostegal membrane greyish. A distinct, vertical lachrymal stripe, continued at an angle, runs through the centre of the eye ; a very faint stripe runs from the posterior orbital margin to the angle of the preoperculum. Dorsal fin greyish, with dark lappets and a dark band along the basal two-thirds of the fin anteriorly, narrowing to the basal third or quarter posteriorly. Caudal dark proximally and along the mid-line. Anal hyaline, with two large, dead-white ocelli. Pelvics black, darkest laterally.

Females and immature males. Ground colour greyish-silver, six or seven faint transverse bars on the flanks and, in some, two bars on the caudal peduncle ; a very faint lachrymal stripe. All fins hyaline.

Boulenger's (1911) account of preserved coloration differs somewhat from that given above, but as his material represented at least two and possibly three species, the discrepancies are not considered significant.

Distribution. Known only from Lake Victoria, unless the locality " Jinja, Ripon Falls " for specimens nos. 1911.3.3.127–130 implies that these fishes were caught *below* the falls in the Victoria Nile.

Ecology. Habitat. The only precise bionomic data available are for those specimens collected by E.A.F.R.O. All these were from one locality, an exposed, shallow and sandy beach near Entebbe Airport.

Food. Thirteen of the sixteen fishes examined had ingested matter in the stomach and intestine ; all these specimens were collected at one locality and at the same time. Except for three fishes, all contained moderately large quantities of bottom debris (sand grains, diatom frustules and fragments of plant tissue) together with fragmentary insect larvae (? Diptera). The exceptional specimens contained only bottom detritus.

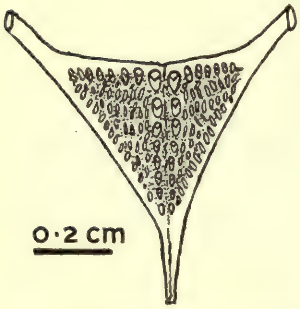

FIG. 3. *Haplochromis pallidus;* lower pharyngeal bone, occlusal view.

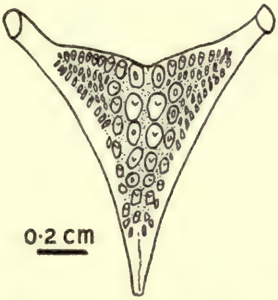

FIG. 4. *Haplochromis riponianus ;* lower pharyngeal bone, occlusal view.

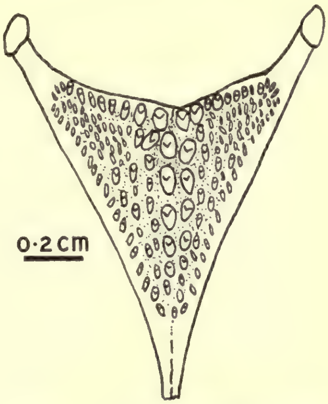

FIG. 5. *Haplochromis saxicola ;* lower pharyngeal bone, occlusal view.

Breeding. Haplochromis pallidus is a female mouth brooder ; the two smallest fishes examined (a male 54 mm. S.L. and a female 58 mm. S.L.) are both adult.

Affinities. Haplochromis pallidus must be considered one of the many small and generalized species in Lake Victoria. Within this group it is extremely difficult to suggest phyletic relationships because the degree of inter-specific differentiation is so slight. In general appearance *H. pallidus* perhaps comes nearest to *H. lacrimosus*, from which species it is distinguished by a higher modal number of gill rakers (9 cf. 8), fewer and somewhat stouter teeth, a lower modal eye/preorbital ratio (1·7 cf. 2·0) and particularly, by differences in the preserved coloration of male fishes. The nature of both oral and pharyngeal dentition suggests that a "*pallidus*"-like species could have been ancestral to the adaptational grade at present represented by *Haplochromis humilior* (see p. 252).

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
Genoa Museum (C.E. 12912) .	Jinja .	Bayon
B.M. (N.H.).—1911.3.3.127–130 .	Jinja, Ripon Falls .	,,
,, 1959.4.28.25–40 .	Entebbe, Airport beach .	E.A.F.R.O.

Haplochromis macrops (Blgr.) 1911

(Text-fig. 6)

Haplochromis stanleyi (part) Boulenger, 1914, *Cat. Afr. Fish.* **3**, 295.
Haplochromis ishmaeli (part) Boulenger, 1914, *tom. cit.* 293.
Tilapia macrops Boulenger, 1911, *Ann. Mus. Genova* (3), **5**, 73. pl. III, fig. 1 ; *Idem*, 1914, *Cat. Afr. Fish.* **3**, 238.
Haplochromis macrops (part, i.e. the species as described but excluding the tentative synonymy of *Astatotilapia jeanneli* Pellegrin), Regan, 1922, *Proc. zool. Soc. London*, 166.

Description, based on forty specimens from Lake Victoria (including the holotype [Genoa Museum] and one of the paratypes) 66–91 mm. S.L.

Depth of body 32·5–38·2 (M = 35·8) per cent of standard length, length of head 31·0–35·1 (M = 33·0) per cent. Dorsal head profile straight or slightly curved, sloping at a moderate angle (*ca.* 35°–40°). Preorbital depth 11·5–16·3 (M = 14·2) per cent of head, least width of interorbital 26·6–32·2 (M = 29·7) per cent. Snout as broad as long or slightly broader, its length 26·6–31·0 (M = 29·0) per cent of head, diameter of eye 28·6–35·4 (M = 33·0) per cent, ratio of eye diameter to preorbital depth 2·0–2·9 (mode 2·3) ; depth of cheek 17·8–24·2 (M = 21·1) per cent of head. Caudal peduncle 14·1–18·4 (M = 16·8) per cent of standard length, 1·2–1·6 (mode 1·4) times as long as deep.

Mouth slightly oblique, posterior tip of the maxilla extending to the vertical to the anterior orbital margin or even as far as the pupil. Lower jaw 38·0–42·5 (M = 39·5) per cent of head, 1·4–2·2 (modal range 1·7–1·8) times as long as broad.

Gill rakers slender or, occasionally, relatively stout ; 8–11 (mode 9) on the lower part of the first arch, the lower 1–4 rakers reduced.

Scales ctenoid ; lateral line with 30 (f.6), 31 (f.17), 32 (f.13) or 33 (f.3) scales ; cheek with 2 or 3 series. Five or 6 (occasionally 7) scales between the lateral line and the dorsal fin origin ; 6 or 7 (occasionally 5, rarely 8) between the pectoral and pelvic fin bases. Scales on the pectoral region (relative to those on the ventral abdominal region) moderate to large.

Fins. Dorsal with 24 (f.6), 25 (f.30) or 26 (f.4) rays, anal with 11 (f.9), 12 (f.30) or 13 (f.1), comprising XV–XVII, 8–10 and III, 8–10 spinous and branched rays for the fins respectively. Pectoral 68·0–96·0 (M = 84·0) per cent of head. Caudal truncate.

Teeth. The outer row of teeth in both jaws (except those situated postero-laterally in the upper) is composed mainly of bicuspid, moderately stout teeth. In certain fishes over 80 mm. S.L. some weakly cuspidate teeth may occur. *H. macrops* is, however, unusual in that the postero-lateral teeth in the upper jaw are generally tricuspid in fishes less than 85 mm. S.L. ; in larger individuals these teeth may be unicuspid. One aberrant individual has only tricuspid teeth in the upper, outer row ; the corresponding row in the lower jaw has a mixture of bi- and tricuspids, with the former predominating. There are 46–66 (mode 60, modal range 56–60) teeth in the upper, outer row.

The inner tooth-rows are made up of tri- and unicuspid teeth arranged in 2 or 3 (rarely 4) rows in the upper jaw and 1 or 2 (less commonly 3) rows in the lower. Inner teeth are implanted so as to stand erect or with a very slight, posteriorly directed slope.

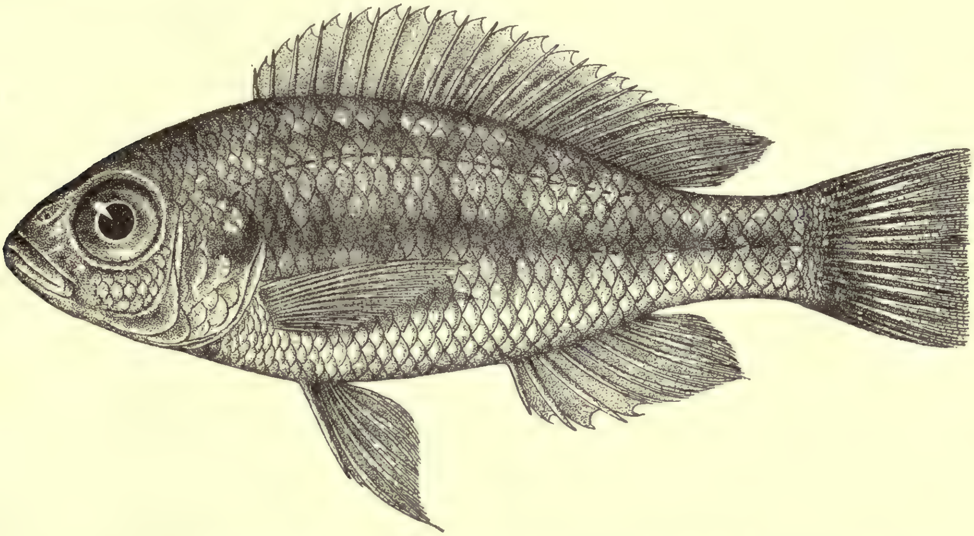

FIG. 6. *Haplochromis macrops ;* holotype (from Boulenger, *Ann. Mus. Genova*).

Lower pharyngeal bone triangular, not enlarged ; teeth fine and cuspidate.

Coloration in life. Sexually active males. Ground colour dusky to intensely black. Dorsal fin black, lappets and margin of the soft part red, as are the spots and blotches between the branched rays. Anal dusky with a diffuse red flush becoming more intense distally : ocelli yellow. Caudal dusky, ventral half with a red flush. Pelvic fins dusky yellow. *Quiescent males* have a female-type coloration, but with yellow anal ocelli and red spots on the soft dorsal. *Females.* Ground colour greyish-yellow to silver-grey. Dorsal and anal fins light yellow, caudal yellowish.

Colour of preserved material. Adult males. Dark blackish-brown, somewhat lighter, except in sexually active fishes, on the chest and branchiostegal membrane ; faint indications of six transverse bars on the flanks (generally not reaching the dorsal and ventral outlines) ; a dark but faint lachrymal stripe is visible in some specimens, as is a faint dark bar along the preoperculum. Dorsal fin dark (especially along the basal third), lappets black. Caudal fin dark. Anal dark on the basal third to half, pale distally, with two or three ocelli. Pelvic fins black. *Females.* Brownish-yellow, some with eight or nine faint transverse bars on the flank and caudal peduncle. All fins hyaline but the caudal somewhat darker.

Distribution. Definite records of *Haplochromis macrops* are available only from Lake Victoria although there is an indication that the species may also occur in the Lake Edward basin. I have examined material identified as *H. macrops* from Lake Edward (one specimen B.M. (N.H.) Reg. No. 1933.2.23.397; see Trewavas, 1933) and from rivers flowing into Lake Edward (see Poll, 1939 and Poll & Damas, 1939). Of these latter specimens (twelve in all) only one (R. G. Mus. Congo 31095, det. David, 1936), from Rutshuru, compares closely with the Victoria population of *H. macrops*. I hesitate to identify the remaining Congo Museum specimens from Rutshuru (Reg. Nos. 64888–64899), but the single specimen from the B.M. (N.H.) seems most closely allied to *H. lividus* Greenwood of Lake Victoria. I have not been able to study the two specimens from Lake Edward (now in Berlin) which Pappenheim & Boulenger (1914) identified as *H. macrops*.

The single specimen (R. G. Mus. Congo 31095) from the Edward basin now referred to *H. macrops* differs slightly from the generality of Victoria fishes in having a somewhat larger eye and longer lower jaw; it is an adult female, 73·0 mm. S.L. The principal morphometric characters of this fish are:

D*	H*	Po. %	Io. %	Eye %	Snt. %	Ck. %	Lj. %	C.P.*	Eye/Po.
32·8	31·4	15·2	30·4	37·0	30·4	21·7	43·4	15·0	2·4

* Per cent standard length.
% Per cent head length.

Dorsal XV, 9; anal III, 9; pectoral 91·3 per cent of head.

In characters of dentition and squamation this fish is similar to those from Lake Victoria.

Ecology. Habitat. The species is apparently confined to the shallow, sandy regions of the lake.

Food. The predominating food organisms in the stomachs and intestines of twenty-four fishes (mainly from one locality, but caught on different occasions) are sub-imaginal Ephemeroptera; two fishes had, however, fed almost exclusively on winged termites (Isoptera) and colonial blue-green algae. Typical bottom debris and sand-grains usually found in the guts of other insectivorous *Haplochromis* were not recorded. The occurrence of sub-imaginal or adult insects and planktonic blue-green algae, together with the absence of bottom debris, suggests that *H. macrops* feeds at the surface or in mid-water. Since the algae were not digested and did not constitute a major proportion of the ingested matter, they may be taken accidentally as the fishes dart after insect prey.

Breeding. *Haplochromis macrops* is a female mouth-brooder. The smallest sexually active fish is a female 73 mm. S.L., the smallest adult male is 78 mm. S.L. It appears that males attain a larger maximum adult size than do females.

Affinities. As with most of the structurally and trophically generalized *Haplochromis* of Lake Victoria, the detailed affinities of *H. macrops* are impossible to determine. The similarities existing between *H. macrops* and *H. cinereus* are discussed elsewhere (p. 242). The two species differ in several characters, particularly in their dentition and the larger eye/preorbital ratio of *H. macrops* (2·0–2·9, mode 2·3, cf. 1·5–1·9, mode 1·8 for *H. cinereus*). Also, the gill rakers of *H. macrops* are finer and more numerous (mode 9) than in *H. cinereus* (mode 7).

The large eye and shallow preorbital of *H. macrops* serve to distinguish the species from most other members of the " generalized species " group.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
Genoa Museum (C.E. 12928) (Holotype)	Bussu	Bayon
B.M. (N.H.).—1911.3.3.137 (Paratype)	Bussu	Bayon
B.M. (N.H.).—1911.3.3.114–115	Jinja, Ripon Falls	,,
,, 1959.4.28.51–78	Beach near Nasu Point	E.A.F.R.O.
,, 1959.4.28.79–84	Buka Bay	,,
	Tanganyika	
,, 1959.4.28.85	Mwanza, Capri Bay	,,
,, 1959.4.28.86	Majita	,,
,, 1959.4.28.87	Beach near Majita	,,

Haplochromis cinereus (Blgr.) 1906
(Text-fig. 7)

Paratilapia cinerea Boulenger, 1906, *Ann. Mag. nat. Hist.* (7), **17**, 439 ; *Idem*, 1907, *Fish. Nile*, 478 ; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 344.
Haplochromis stanleyi (part), Boulenger, 1915, *tom. cit.*, 295.
Tilapia lacrimosa (part) Boulenger, 1906, *Ann. Mag. nat. Hist.* (7), **17**, 450 ; *Idem*, 1915, *tom. cit.*, 234.
Haplochromis cinereus (part), Regan, 1922, *Proc. zool. Soc. London*, 166.
Haplochromis melanopus (part), Regan, 1922, *op. cit.* 165.

Description, based on twelve specimens (including the holotype) 71–81 mm. S.L.

Depth of body 34·6–39·0 per cent of standard length, length of head 30·8–37·3 (M = 34·7) per cent. Dorsal head profile straight or slightly curved, sloping at *ca.* 40°–50°. Preorbital depth 15·0–18·0 (M = 16·4) per cent of head length, least interorbital width 23·3–28·0 (M = 25·3) per cent. Snout as long as broad or slightly longer, its length 29·2–34·6 (M = 32·2) per cent of head, eye diameter 26·2–32·0 (M = 28·7) per cent, ratio of eye diameter to preorbital depth 1·5–1·9 (mode 1·8). Depth of cheek 20·8–26·0 (M = 23·0) per cent of head. Caudal peduncle 15·7–18·7 per cent of standard length, 1·4–1·6 times as long as deep.

Mouth horizontal or very slightly oblique; jaws equal anteriorly, the lower 34·6–41·3 (M = 37·7) per cent of head and 1·4–1·8 (mode 1·6) times as long as broad. Lips slightly thickened. Posterior tip of the maxilla extending almost to the vertical through the anterior orbital margin or as far as the eye.

Gill rakers moderately stout, 7–9 (mode 7) on the lower part of the first gill-arch, the lowermost two or three rakers reduced.

Scales ctenoid; lateral line with 30 (f.1), 31 (f.1), 32 (f.4) or 33 (f.6) scales; cheek with 3 or 4 series; 5–6½ scales between the lateral line and the dorsal fin origin; 7 or 8 (rarely 6 or 9) between the pectoral and pelvic fin bases. Scales on the pectoral region small or, less frequently, moderate.

Fins. Dorsal with 24 (f.8) or 25 (f.4) rays, anal with 11 (f.4) or 12 (f.8), comprising XV or XVI, 9 or 10 and III, 8 or 9 spinous and branched rays for the fins respectively. Caudal truncate. Pectoral 72·5–92·0 (M = 80·2) per cent of head.

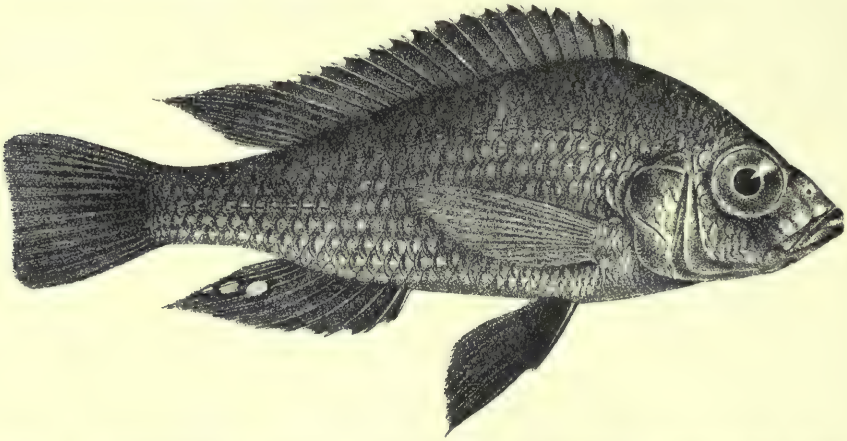

FIG. 7. *Haplochromis cinereus*; holotype (from Boulenger, *Fishes of the Nile*).

Teeth. Teeth in the outer row of both jaws are weakly bicuspid or unicuspid, relatively stout and slightly recurved; in most fishes there is an admixture of both types, with unicuspids predominating. There are 40–54 teeth in the upper, outer row.

The inner series are composed of either unicuspid or bicuspid teeth; less commonly there is a mixture of both types. A characteristic feature of the inner tooth-rows is the way in which the teeth are implanted obliquely so that the crowns point posteriorly. Three or 4 (rarely 2) inner rows occur in the upper jaw and 2 or 3 in the lower.

The dentition of *H. cinereus* is unlike that of other species in the "generalized species" group; it is, indeed, typical of the dentition found throughout the large group of piscivorous predators. However, in other characters (syncranial architecture, feeding habits and body-form) *H. cinereus* is one of the generalized species (see p. 242).

Lower pharyngeal bone triangular, the dentigerous surface slightly broader than long. Teeth in the two median rows are slightly enlarged in five of the specimens examined, but are slender in the remaining seven fishes; the other pharyngeal teeth are slender in all specimens.

Coloration in life unknown. *Colour of preserved fishes: Adult males.* Ground colour greyish-brown; chest and branchiostegal membrane dusky; a faint lachrymal stripe. All fins hyaline, with very faint indications of dark maculae on the soft dorsal; dorsal lappets dark. Anal fin with two or three whitish ocelli (orange surrounded by red in newly preserved material, according to Boulenger). Pelvics black except for a large light area extending over the distal half but not including the first branched ray. *Females.* Brownish, silvery grey ventrally, with eight or nine dark transverse bars on the flanks and caudal peduncle. All fins hyaline, the basal third to half of the caudal weakly maculate.

Distribution. Known only from Lake Victoria.

Ecology. No ecological data (except the locality) are available for the three specimens collected by Degen. The remaining nine fishes were caught in water less than 20 feet deep, over a sandy bottom on both protected and exposed shores.

Food. The stomach and intestinal contents of ten specimens (from four localities) were examined. Of these, three were empty and the remainder yielded sand-grains, bottom detritus (including fragments of plant epidermis) and some larvae of dipterous insects.

Breeding. The species is a female mouth-brooder. The smallest specimens available (a male and a female 71 mm. S.L.) are both sexually mature. As far as can be determined from this inadequate sample, both sexes reach the same adult size.

Discussion of affinities and synonymy. In Regan's revision of the Lake Victoria *Haplochromis* (1922) the definition of *H. cinereus* was expanded to embrace a number of small and generalized or near-generalized forms previously recognized as distinct species. The first attempt to prune this complex was Lohberger's resurrection of *H riponianus* (see p. 252). Now, with more specimens available and some knowledge of *Haplochromis* in nature, it is clear that Regan's definition of *H. cinereus* must be narrowed considerably and that a further two species (*H. lacrimosus* and *H. pallidus*) should be resurrected. Amongst the group of anatomically and trophically unspecialized *Haplochromis* in Lake Victoria, *H. cinereus* is unusual because of its oral dentition (see p. 240). Relatively stout, clearly bicuspid teeth in the outer series of the jaws and erect tricuspid inner teeth are usual in the generalized species. The dentition of *H. cinereus,* on the other hand, shows a marked tendency for slender, unicuspid teeth to predominate in the outer rows; the few bicuspid teeth present are weakly cuspidate. The inner teeth of *H. cinereus* are also atypical for the group in that the usual erect and tricuspid form is largely replaced by slender unicuspids implanted so as to point posteriorly. In fact, the dentition of *H. cinereus* is very like that of many predatory species. With so few specimens of *H. cinereus* known it is impossible to generalize on its feeding habits; however, the gut contents of seven fishes from four different localities do not even hint at the species being a piscivorous predator.

At this point it should perhaps be stressed that my observations are confined to adult fishes 70–90 mm. long ; juveniles have still to be discovered.

Because " *Haplochromis cinereus* " had become something of a dumping ground for any small *Haplochromis* species or specimen, the published information (Graham, 1929) on distribution and habitats can no longer be considered reliable. I have examined " *H. cinereus* " material collected by Graham and find that none of these specimens is referable to *H. cinereus, sensu stricto.* The bulk of this material is of undescribed species and will be dealt with in subsequent papers. Thus, Graham's remark that " the species (*H. cinereus*) is therefore widely distributed except in the deepest part of the lake " and Brooks' (1950, p. 159) elaboration of these data do not apply to *H. cinereus* but rather to the whole species-complex of generalized, bottom feeding *Haplochromis* in the lake.

Haplochromis cinereus has been cited as representing the ancestral type from which the present species-flock could have evolved (Regan, 1922 ; Greenwood, 1951). For the reasons mentioned above this concept must be abandoned ; there are several other *Haplochromis* species still surviving in Lake Victoria which are structurally closer to the ancestral type, for example *H. lacrimosus*, *H. nubilus* or *H. pallidus.*

The particular affinities of *H. cinereus* are difficult to determine. In gross anatomy and appearance *H. cinereus* does not differ markedly from the majority of small *Haplochromis* ; only when its dentition is considered does the difference appear striking. Like so many members of the generalized group, *H. cinereus* seems to be an independent offshoot from one of the basic stocks.

In overall appearance and perhaps in at least some ecological requirements *Haplochromis macrops* is the one extant species most like *H. cinereus.* The two species are differentiated principally by the larger eye, shallower preorbital and the stouter, more numerous outer teeth of *H. macrops.*

Haplochromis cinereus is not, as Regan suggested, closely related to *H. ishmaeli.* To stress this supposed relationship, Regan noted that six of the *H. ishmaeli* syntypes were actually specimens of *H. cinereus.* As a result of this present revision none of these specimens is still retained in *H. cinereus. Haplochromis ishmaeli* belongs to a distinct phyletic line, discussed more fully on pages 269 and 273.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.292 (Holotype)	Buganga	Degen
B.M. (N.H.).—1906.5.30.350	Entebbe	,,
,, 1906.5.30.482	Bunjako	,,
,, 1959.4.28.41	Entebbe, Harbour	E.A.F.R.O.
,, 1959.4.28.48–50	Entebbe, Airport beach	,,
	Tanganyika	
,, 1959.4.28.42–47	Mwanza, Capri Bay	E.A.F.R.O.

Haplochromis niloticus nom. nov.

(Text-fig. 8)

Tilapia bayoni Boulenger, 1911, *Ann. Mus. Genova* (3), **5**; 72, pl. III, fig. 2 (*nec Paratilapia bayoni* [= *Haplochromis bayoni* (Blgr.), see Regan, 1922, p. 176] Blgr., 1909, *Ann. Mus. Genova* (3), **4**, 304, fig.

Haplochromis humilior (part), Regan, 1922, *Proc. zool. Soc. London*, 169.

Description, based on the holotype (100 mm. S.L.) and two other specimens 96 and 102 mm. S.L.

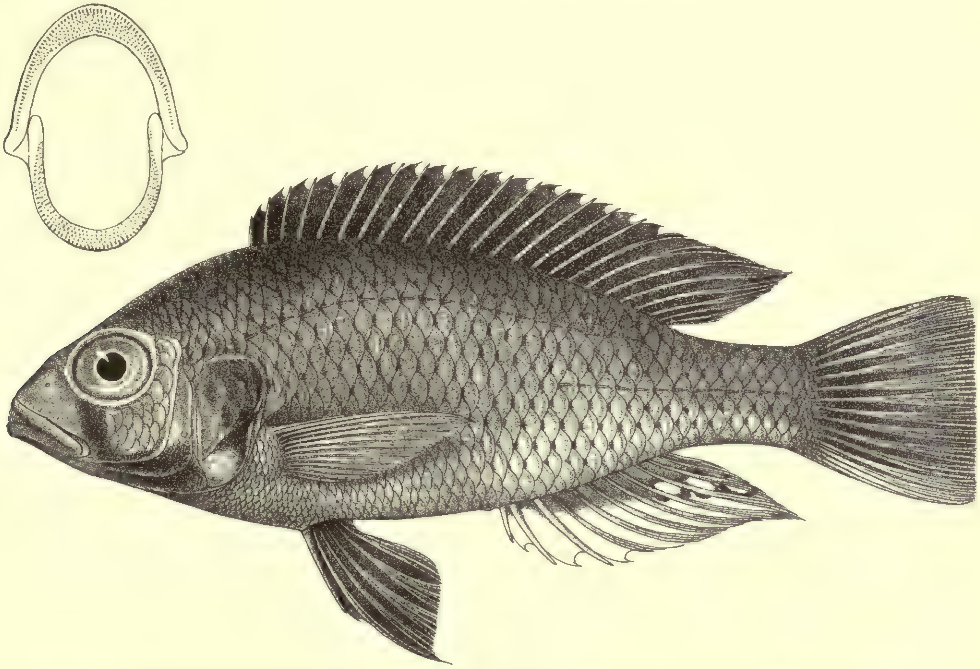

FIG. 8. *Haplochromis niloticus*; holotype (from Boulenger, *Ann. Mus. Genova*).

The principal morphometric characters are given below :

S.L.	Depth*	Head*	Po. %	Io. %	Snt. %	Eye %	Ck. %	Lj. %	C.P.*
96·0	35·4	33·3	17·2	21·8	31·3	31·3	20·4	39·0	18·2
†100·0	33·0	33·0	15·2	24·3	30·3	33·5	24·0	33·3	17·5
102·0	34·3	33·8	17·4	24·7	29·0	30·5	23·2	37·7	17·1

† Holotype.
% Per cent. of head length.
* Per cent. of standard length.

Dorsal head profile sloping rather steeply (*ca.* 45°–50°) and slightly curved. Mouth horizontal; jaws equal anteriorly, the length/breadth ratio of the lower 1·6–1·9. Posterior tip of the maxilla extending to the vertical through the anterior part of the eye. Lips not markedly thickened.

Gill rakers moderately stout ; 7 or 8 (the lowermost one or two reduced) on the lower part of the first arch.

Scales ctenoid ; 32 in the lateral line ; cheek with 2 or 3 series. Six or 7 scales between the lateral line and the dorsal fin origin, 8 or 9 between the pectoral and pelvic fin bases ; scales on the pectoral region small.

Fins. Dorsal with 25 (f.2) or 26 (f.1) rays, anal with 12, comprising XVI, 9–10 and III, 9 spinous and branched rays for the fins respectively. Pelvic fins with the first branched ray only slightly produced and extending to the origin of the anal. Caudal sub-truncate, scaled only on its proximal half.

Teeth. The outer row in both jaws is composed of moderately slender, movably implanted and unequally bicuspid teeth ; the most posterior five or six teeth in the upper jaw are caniniform and stouter than those situated anteriorly and laterally. There are 65–70 teeth in the upper, outer series.

Teeth in the inner series are small and tricuspid, and are arranged in four or five rows in the upper jaw and four in the lower. The interspace between the inner and outer series is very narrow.

Lower pharyngeal bone triangular, slender or slightly enlarged, the two median rows of teeth relatively coarse in two specimens (including the holotype) and somewhat more enlarged in the third. In the latter fish the next lateral row of teeth is also enlarged and the most posterior teeth of the median rows are sub-molariform.

Osteology. A complete skeleton was prepared from one of the specimens caught at the same time as the three fishes described above. However, since *H. niloticus* is very similar to *H. nuchisquamulatus* (which also occurs in the Victoria Nile) it is difficult to confirm the specific identity of the skeleton. Apparently the sole diagnostic osteological character is the lower pharyngeal bone, which is slender in *H. nuchisquamulatus* and slightly thickened in *H. niloticus.* The lower pharyngeal of the skeleton is that of *H. niloticus* and on this character alone the skeleton is referred to *H. niloticus.* In all other characters, except the oral dentition, the skeleton of *H. niloticus* resembles that of a generalized *Haplochromis* species. There are 14 + 16 vertebrae.

Coloration of live fishes is unknown. The three preserved specimens are all apparently males (judging from the well-defined anal ocelli) and adult. Because most of the coloration is now lost (the fishes are a uniform brownish-grey) I quote the description given by Boulenger (1911) of the then newly preserved specimens. " Back dark olive to blackish, sides brassy yellow to coppery red ; a more or less distinct black bar below the eye ; dorsal and ventrals brown to black ; anal pink, blackish at the base, usually with two or three large orange ocellar spots ; caudal brown or blackish the lower third often pink." From this description the coloration of male fishes seems to be remarkably like that of *H. humilior* from Lake Victoria (see p. 250).

Distribution. Haplochromis niloticus is known only from the Victoria Nile ; no information is available on its habitat or on feeding and breeding habits.

Affinities. Haplochromis niloticus has been compared with two *Haplochromis* species from Lake Victoria. In his original description, Boulenger compared the species with *H. martini*, whilst Regan (1922) considered *H. niloticus* to be conspecific with *H. humilior*. In my opinion *H. martini* and *H. humilior* are not closely related to one another and *H. niloticus* is not allied to either. The three species differ in several fundamental characters, especially in the nature of their dentition. Admittedly, the somewhat enlarged median pharyngeal teeth of *H. niloticus* approach the condition found in some specimens of *H. humilior*, but the oral dentition of the two species is very dissimilar. The outer teeth are finer and more numerous in *H. niloticus* and there are more rows of inner teeth barely separated from the outer row. These same characters, together with a somewhat different arrangement of the jaw skeleton, serve to separate *H. niloticus* from *H. martini*.

The nature of the dentition in *H. niloticus* suggests affinity with *H. nigricans* and *H. nuchisquamulatus*, particularly the latter. From *H. nigricans*, *H. niloticus* is distinguished by its more generalized neurocranium and dentary (see Greenwood, 1956*b*) and its slightly enlarged lower pharyngeal teeth. From *H. nuchisquamulatus*, *H. niloticus* is again distinguished by having somewhat enlarged pharyngeal teeth and by a narrower interorbital region.

The affinities of *H. niloticus* are not especially obvious ; the species is probably yet another slightly specialized side branch from the generalized *Haplochromis* stem.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
Genoa Museum (C.E. 12932) (Holotype *T. bayoni* Blgr. 1911)	Kakindu, Victoria Nile	Bayon
B.M. (N.H.).—1911.3.3.124–5	,, ,,	,,
,, 1911.3.3.126 (skeleton)	,, ,,	,,

Haplochromis martini (Blgr.) 1906
(Text-fig. 9)

Tilapia martini, Boulenger, 1906, *Ann. Mag. nat. Hist.* (7), **17**, 449.
T. martini (part), *Idem*, 1914, *Cat. Afr. Fish.* **3**, 239, fig. 158.
Haplochromis martini, Regan, 1922, *Proc. zool. Soc. London*, 171.

Regan (1922) based his redescription of *H. martini* on three of the six syntypes, but did not indicate to what species he referred the remaining type specimens. However, amongst the material Regan identified as *H. cinereus* there are three type specimens of *T. martini* (B.M. (N.H.) Reg. No. 1906.5.30.466–468). Presumably it was Regan's intention to include these in the published synonymy of *H. cinereus*. The three specimens are not *H. cinereus* but are, in fact, *Haplochromis martini*.

Lectotype. A brooding female 88 mm. standard length (B.M. (N.H.) Reg. No. 1906.5.30.465) from Bunjako, Uganda.

Description, based on twenty-nine specimens (including the lectotype and four paratypes) 59–104 mm. S.L.

Depth of body 30·8–38·0 (M = 34·4) per cent of standard length, length of head 31·0–38·1 (M = 35·4) per cent. Dorsal head profile very strongly decurved, the snout sloping at an angle of *ca.* 50°–70°. Depth of preorbital 13·0–20·0 (M = 16·6) per cent of head, least interorbital width 20·4–26·8 (M = 24·1) per cent. Snout slightly longer than broad, its length 27·3–34·4 (M = 30·2) per cent of head; diameter of eye 29·4–37·5 (M = 31·7) per cent, depth of cheek 20·4–27·7 (M = 24·6) per cent. Caudal peduncle 15·3–20·6 (M = 17·3) per cent of standard length, 1·2–1·8 (mode 1·6) times as long as deep.

Jaws equal anteriorly, the lower 38·4–45·8 (M = 42·6) per cent of head, 1·6–2·1 (modal range 1·7–2·0) times as long as broad; mouth horizontal or slightly oblique. Posterior tip of the maxilla extending to the vertical through the pupil or, less commonly, only to the anterior part of the eye. Such a marked posterior extension of the maxilla is unusual in Lake Victoria *Haplochromis* and may be considered one of the diagnostic characters of *H. martini.*

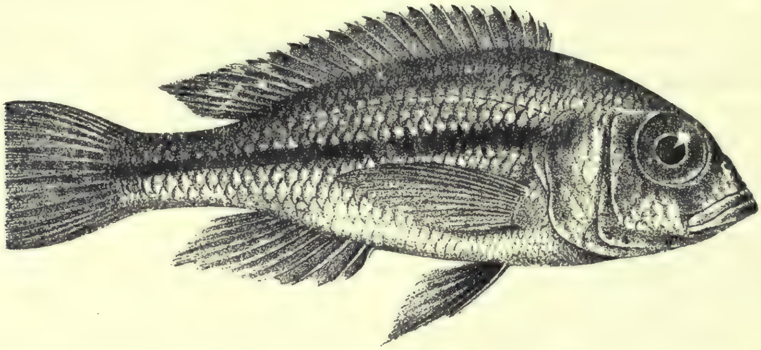

FIG. 9. *Haplochromis martini ;* lectotype (from Boulenger, *Fishes of the Nile*).

Gill rakers on the first arch moderately stout (but rather slender in a few specimens), one or two of the uppermost often flattened and bifid; 8 or 9, rarely 7 or 10 (mode 9) gill rakers on the lower part of the arch.

Scales ctenoid; lateral line with 31 (f.5), 32 (f.7), 33 (f.9), 34 (f.7) or 35 (f.1) scales; cheek with 3 or 4 rows. Six to 8 scales between the lateral line and the dorsal fin origin, 7 or 8 (rarely 6) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.9), 25 (f.19) or 26 (f.1) rays, anal with 11 (f.8), 12 (f.19) or 13 (f.2), comprising XIV–XVI, 8–10 and III, 8–10 spinous and branched rays for the fins respectively. Pectoral fin 73·5–86·5 (M = 82·0) per cent of head; caudal truncate or sub-truncate.

Teeth. In the outer row of both jaws the teeth are slender and mainly unequally bicuspid in fishes less than 85 mm. S.L. Above this size both weakly bicuspid and unicuspid teeth occur together. In fishes of all sizes a few tricuspid teeth are found postero-laterally in the upper jaw, an uncommon character in Lake Victoria *Haplochromis* (see *H. macrops*, p. 237). There are 46–76 teeth in the upper jaw (ill-defined modal range 68–70).

Tricuspid teeth predominate in the inner series although in one large fish (101 mm. S.L.) the inner teeth are all unicuspid. The inner series are arranged in 2 (less commonly 3) rows in the upper jaw and in 1 or 2 (less commonly 3) rows in the lower.

Lower pharyngeal bone triangular, not enlarged and with slender, cuspidate teeth.

Osteology. The neurocranium does not differ greatly from the generalized *Haplochromis* type, but the premaxilla has relatively longer dentigerous arms.

Coloration in life. Sexually active males. Ground colour golden-yellow, shading to silvery-white, with three or four faint black blotches below the insertion of the dorsal fin, and a distinct coppery sheen on the nape and anterior part of the flank. Dorsal fin hyaline, with a pinkish flush. Distal half of the anal scarlet, the proximal half colourless ; anal ocelli orange-red. Caudal fin flushed with scarlet, especially intense on the distal half. Pelvics dark on the outer half, reddish-yellow mesially. *Quiescent males* golden-yellow shading to silvery-white ventrally ; a fairly distinct dark mid-lateral stripe and an interrupted upper stripe slightly below the insertion of the dorsal fin. Dorsal and caudal fins darkish, the anal and pelvics lighter ; anal ocelli yellow. *Females and juvenile males*. Ground colour and banding as above, the upper band usually broken into rather indistinct blotches. All fins light yellow, the caudal somewhat darker.

Preserved material. Both sexes. Ground colour yellowish-silver to brownish, an intense, narrow mid-lateral black line extends from the upper angle of the operculum to the caudal peduncle and, in some specimens even on to the caudal fin ; a fainter, often interrupted black stripe runs mid-way between the upper lateral line and the dorsal fin base. In some fishes there are traces of a very faint interocular band. All fins hyaline ; in males the dorsal has dusky lappets and the pelvics are dark.

Distribution. *Haplochromis martini* is known only from Lake Victoria. Specimens from Lake Edward once identified as *Tilapia martini* (Boulenger, 1914) were later referred to *H. schubotzi* (Regan, 1921).

Ecology. Habitat. Available records (from eight localities) suggest that *H. martini* is restricted to water less than 40 feet deep, where the species is ubiquitous but nowhere common. The species has been found over both sand and mud bottoms, on exposed shores and in sheltered bays. There are some indications that it may not occur close inshore since the only record of *H. martini* in beach-operated seine nets came from an area (Majita) where the nets were shot about 300 yards off-shore.

Food. Sixteen of the twenty-two specimens examined had ingested material in the stomach and intestines ; in three of these specimens, however, the contents were unidentifiable sludge. Eleven of the remaining thirteen fishes contained, as the exclusive or predominating food, the fragmentary remains of small fishes (identified in two cases as *Haplochromis*) ; one of these individuals had also fed on larval Diptera and another had eaten what appeared to be the foot and other soft parts of a snail. Another fish had fed only on larval Diptera and one was empty except for some small fish bones in the posterior intestine.

Breeding. *Haplochromis martini* is a female mouth-brooder ; females reach sexual maturity at *ca*. 80 mm. S.L. ; no data are available for males. Both sexes appear to attain the same maximum adult size.

Affinities. Because of its strongly decurved snout, large eye and the marked posterior extension of the premaxilla, *H. martini* is one of the more immediately recognizable species. Yet, despite these characters *H. martini* retains most of the fundamental features of a generalized species such as *H. macrops*. On the other hand, *H. martini* differs from members of this species group (and probably most other Lake Victoria species) in its bright yellow coloration.

When attempting to assess the phyletic affinities of *H. martini* one is faced with these rather contradictory characters and with the fact that, despite its generalized dentition and body-form, *H. martini* can be a piscivorous predator. The majority of piscivorous *Haplochromis* in Lake Victoria are larger than *H. martini* and have elongate bodies and heads ; the teeth in these species are usually large and caniniform.

Taking into account the various structural and ecological characters *H. martini* should perhaps be considered a superficially but trophically distinct branch from the generalized stem as represented, perhaps, by an *H. macrops*-like ancestor.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.463–5 (Lectotype and paratypes)	Bunjako	Degen
,, 1906.5.30.466–8 (Paratypes)	,,	,,
,, 1959.4.28.124–132	Pilkington Bay	E.A.F.R.O.
,, 1959.4.28.138	Old Bukakata Bay	,,
,, 1959.4.28.140	Napoleon Gulf, near Jinja	,,
	Tanganyika	
,, 1959.4.28.116–123	Majita	,,
	Kenya	
,, 1959.4.28.133–137	Off Port Southby	,,
,, 1959.4.28.139	Beach below Usoma Lighthouse	,,

Haplochromis humilior (Blgr.) 1911

(Text-figs. 10 and 11)

Tilapia humilior Boulenger, 1911, *Ann. Mus. Genova* (3), **5**, 74, pl. III, fig. 3.
Tilapia lacrimosa (part), Boulenger, 1915, *Cat. Afr. Fish.* **3**, 234.
Haplochromis desfontainesii (part), Boulenger, 1915, *tom. cit.*, 303.
Haplochromis nubilus (part), Regan, 1922, *Proc. zool. Soc. London*, 164.
Haplochromis humilior (part), Regan, 1922, *op. cit.*, 169.
? *Paratilapia granti* (part), Boulenger, 1915, *tom. cit.*, 342.

Lectotype. A male 90 mm. standard length from Kakindu, Victoria Nile, collected by Bayon (now in the collections of the Museo Civico di Storia Naturale, Genoa).

Description, based on thirty specimens 65–90 mm. S.L. (including the lectotype and one paratype; the second paratype [B.M. (N.H.) Reg. No. 1911.3.3.152] is very poorly preserved and although examined, is not included in the description).

Depth of body 29·0–37·5 (M = 34·4) per cent of standard length, length of head 31·6–37·8 (M = 34·7) per cent. Dorsal head profile curved, sloping at an angle of 45°–50°. Preorbital depth 13·6–17·9 (M = 16·3) per cent of head, least interorbital width 21·0–28·6 (M = 24·2) per cent. Snout as long as broad or slightly longer, its length 27·0–34·8 (M = 30·9) per cent of head, diameter of eye 27·0–32·5 (M = 30·3), depth of cheek 18·5–23·2 (M = 21·2) per cent. Caudal peduncle 15·2–19·1 (M = 17·4) per cent of standard length, 1·3–1·8 (mode 1·5) times as long as deep.

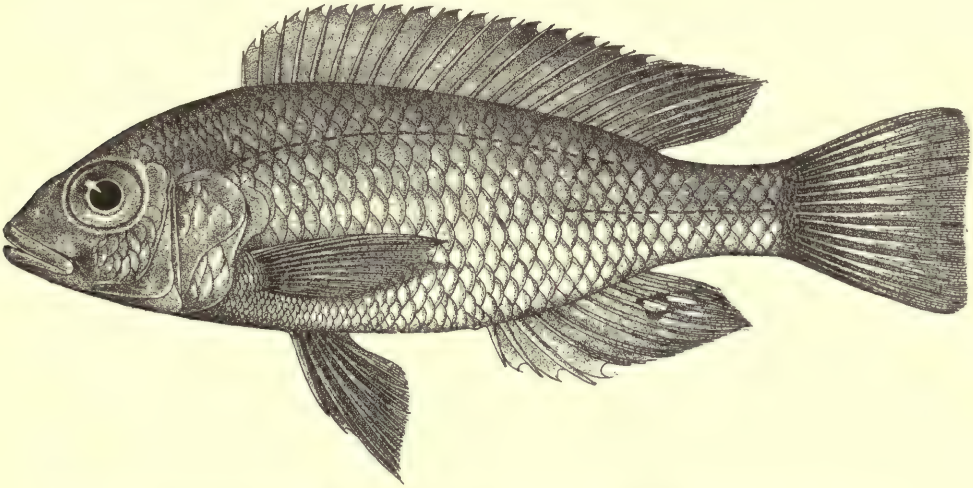

FIG. 10. *Haplochromis humilior*, lectotype (from Boulenger, *Ann. Mus. Genova*).

Mouth horizontal, the lower jaw often slightly shorter than the upper; length of lower jaw 33·4–39·6 (M = 36·6) per cent of head and 1·3–2·2 (modal range 1·5–1·8) times as long as broad. Posterior tip of the maxilla extending to the vertical through the anterior orbital margin or somewhat beyond (to below the pupil in one specimen).

Populations of *H. humilior* from different localities in the lake appear to have characteristic facies which make any one population more or less readily identifiable; unfortunately no means of quantifying these characters could be determined. Also, it has so far proved impossible, through lack of material, to decide whether Lake Victoria *H. humilior* differ from those inhabiting the Victoria Nile.

Gill rakers short and stout, 6–8 (modes 6 and 7), rarely 9 on the lower part of the first arch.

Scales ctenoid; lateral line with 30 (f.7), 31 (f.7), 32 (f.7) or 33 (f.7) scales; cheek with 2 or 3 (rarely 4) series. Six or 7 scales between the lateral line and the origin of the dorsal fin, 6–8 (rarely 5 or 9) between the pectoral and pelvic fin bases. Scales on the pectoral region relatively small.

Fins. Dorsal with 24 (f.6), 25 (f.21) or 26 (f.3) rays, anal with 11 (f.4) or 12 (f.24) comprising XV–XVI, 8–10 and III, 8 or 9 spinous and branched rays for the fins respectively. Pectoral 69·0–92·3 (M = 81·0) per cent of head. Caudal truncate.

Teeth. The outer teeth in both jaws are moderately stout and unequally or, less frequently, sub-equally bicuspid. In fishes over 70 mm. S.L. some weakly bicuspid or even unicuspid teeth may occur ; there are 36–52 (modal range 46–48) teeth in the upper, outer series.

Inner teeth are tricuspid and arranged in 2 or 3 (rarely 4) rows in the upper jaw and 1 or 2 (rarely 4) in the lower. A distinct space separates the inner and outer tooth series.

Lower pharyngeal bone and teeth. The lower pharyngeal bone, although relatively stout is less massive than the bone in a specimen of *H. ishmaeli* or *H. pharyngomylus* of the same size. Teeth in the two median rows are always enlarged, with the most posterior one or two pairs largest. There is some variation in the degree of enlargement of the median teeth, which may be bicuspid, conical or even molariform ; no clear-cut correlation could be detected between, on the one hand, tooth-size and form and, on the other, the sex and size of the fish. There is, however, a tendency for larger individuals to have the coarsest median pharyngeal teeth. Sagittal sections through a number of bones (from fishes 65–70 mm. S.L.) suggest that both time and chance may influence the nature of the dentition, since unerupted replacement teeth are always molariform irrespective of the nature of the functional teeth which they underlie.

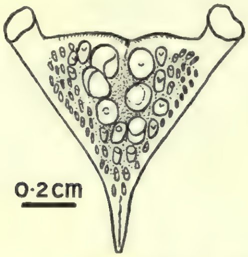

FIG. 11. *Haplochromis humilior ;* lower pharyngeal bone, occlusal view, from a Lake Victoria specimen.

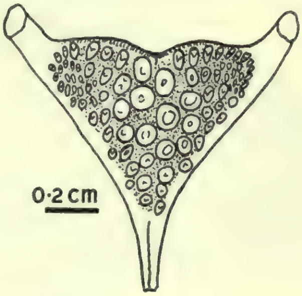

FIG. 12. *Haplochromis theliodon ;* lower pharyngeal bone, occlusal view.

In addition to the two median rows, the next lateral row on each side may also contain a number of molariform teeth.

Coloration in life. Breeding males. Ground colour dark silvery-grey with intense dusky blotches on the head ; branchiostegal membrane dull black. A coppery flush extends over the cheek, operculum and flank as far as the origin of the anal fin. Anal and caudal fins light red, the colour becoming more intense along the margins of both fins and the upper and lower posterior angles of the caudal; two or three yellow anal ocelli. Dorsal fin dusky, with an orange-red margin to the soft part and red spots and bars between the rays of the posterior half of the spinous dorsal and over the entire soft part. Pelvics black. *Quiescent males.* General coloration as in females except that the pelvics are somewhat dusky and the unpaired fins have a pinkish flush; anal ocelli are present. *Females.* Ground colour silvery-yellow. Dorsal, pelvic and anal fins pale yellow, the dorsal with red spots distributed as in males.

Colour of preserved material. Males. Greyish, darker dorsally, the chest and branchiostegal membrane sooty; in some specimens there are traces of seven or eight, narrow transverse bars on the flank and caudal peduncle. A lachrymal stripe, a pair of transverse stripes across the snout and, in some fishes, a broad band across the interorbital region are also visible, as are one or two bands on the nape. Dorsal fin variable, from hyaline to dusky. Anal hyaline in quiescent fishes and whitish in active individuals. Pelvics black (darkest in active fishes) but with a whitish overlay on the proximal half. *Females* silvery, some with very faint traces of vertical bars usually most obvious on the mid-lateral aspects of the flanks. All fins hyaline.

Distribution. The species occurs in Lake Victoria and the Victoria Nile.

Ecology. Habitat. In Lake Victoria the species is confined to shallow water over sandy beaches in both exposed and sheltered areas. No data are available for the riverine populations.

Food. The gut contents of thirty-two fishes (from two localities) yielded identifiable material. Of these specimens, twenty-four contained bottom debris (sand grains, plant fragments, diatom frustules and blue-green algae) together with remains of both larval and pupal insects (especially Diptera and Trichoptera, less frequently, Ephemeroptera); four fishes contained only insect remains and one only the diatom *Melosira.* Ten individuals had eaten, in addition to insects, both bivalves (unidentifiable) and gastropods (*Melanoides* sp. and *Bellamya* sp.). These molluscan fragments were too finely divided to allow for any estimate of the number of animals eaten. Nevertheless it does seem, from this sample at least, that Mollusca are not a major element in the food of *H. humilior.*

The large quantities of sand found with the remains of Trichoptera larvae in most fishes is of interest, particularly since the grains are small and of a remarkably uniform size. This suggests that the sand grains could be derived from the sand-grain cases made by certain caddis larvae. The moderately large pharyngeal mill of *H. humilior* may thus serve the dual purpose of crushing mollusc shells and the sand-grain cases of certain larval insects.

Breeding. Nothing is known about the breeding habits of *H. humilior.* The smallest specimens available (a male and a female both 65 mm. S.L.) are adult; the sexes apparently do not differ in maximum adult size attained.

Affinities. Haplochromis humilior differs from the generality of small *Haplochromis* species in several characters, particularly in having a relatively massive lower pharyngeal bone and in having a low modal number of gill rakers (6–7). Another pronounced difference lies in the tendency for the lower jaw to be shorter than the upper. In most other characters, *H. humilior* resembles *H. pallidus*, a species which shows incipient hypertrophy of the lower pharyngeal bone. *Haplochromis humilior* could be a more specialized off-shoot from an *H. pallidus*-like stem. Unlike many other presumed phyletic lines within the Victoria species flock, this one is not continued by one or more extant species. *Haplochromis humilior* does not appear to have any close relationship to the principal group of species with enlarged pharyngeals, namely *H. obtusidens*, *H. ishmaeli* and *H. pharyngomylus*.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
Genoa Museum (C.E. 12910) (Lectotype)	Kakindu, Victoria Nile	Bayon
B.M. (N.H.).—1911.3.3.152–3 (Paratypes)	,, ,,	,,
,, 1906.5.20.314	Entebbe	Degen
,, 1959.4.28.88–107	Beach near Nasu Point	E.A.F.R.O.
,, 1959.4.28.108	Near Grant Bay	,,
,, 1959.4.28.109–112	Entebbe, Harbour	,,
	Tanganyika	
,, 1959.4.28.113–115	Majita	,,
	Kenya	
,, 1909.11.15.38	Kisumu Bay	Blayney-Percival

Haplochromis riponianus (Blgr.) 1911

(Text-figs. 4 and 13)

Pelmatochromis riponianus (part) Boulenger, 1911, *Ann. Mus. Genova* (3), **5**, 69, pl. II, fig. 3; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 411, fig. 280.
Haplochromis riponianus, Lohberger, 1929, *Zool. Anz.* **86**, 222.
Paratilapia serranus (part), Boulenger, 1915, *tom. cit.*, 334.
Paratilapia victoriana (part), Boulenger, 1915, *tom. cit.*, 341.
Haplochromis ishmaeli (part) Boulenger, 1906, *Ann. Mag. nat. Hist.* (7), **17**, 446; *Idem*, 1915, *tom. cit.* 293.
Haplochromis cinereus (part), Regan, 1922, *Proc. zool. Soc. London*, 166.

On the basis of specimens in the Vienna Museum, Lohberger (1929) decided that Regan's views on the conspecificity of *Pelmatochromis riponianus* and *H. cinereus* could not be substantiated; consequently he resurrected the former species as *Haplochromis riponianus*. I have not examined Lohberger's specimens but, from studying considerably more material than was available to either Regan or Lohberger, I can fully endorse the latter's action.

Lectotype. A male 95·5 mm. standard length, from Jinja, Uganda, collected by Bayon (Genoa Museum, C.E. 12996).

Description, based on twenty-eight specimens (including the lectotype and two paratypes) 57–104 mm. S.L. One other paratype (B.M. (N.H.) Reg. No. 1911.3.3.37) is not included in the description.

Depth of body 33·3–39·4 (M = 35·7) per cent of standard length, length of head 32·8–37·7 (M = 35·7) per cent. Dorsal head profile straight or very slightly curved, sloping at an angle of *ca.* 35°–45°. Preorbital depth 16·3–19·5 (M = 17·6) per cent of head, least interorbital width 23·0–28·1 (M = 25·1) per cent. Snout slightly longer than broad, its length 30·5–35·4 (M = 33·6) per cent of head; diameter of eye 24·2–31·0 (M = 26·6), depth of cheek 19·2–25·0 (M = 22·7) per cent. Caudal peduncle 14·4–18·4 per cent of standard length, 1·2–1·7 times as long as deep (modal range 1·3–1·5).

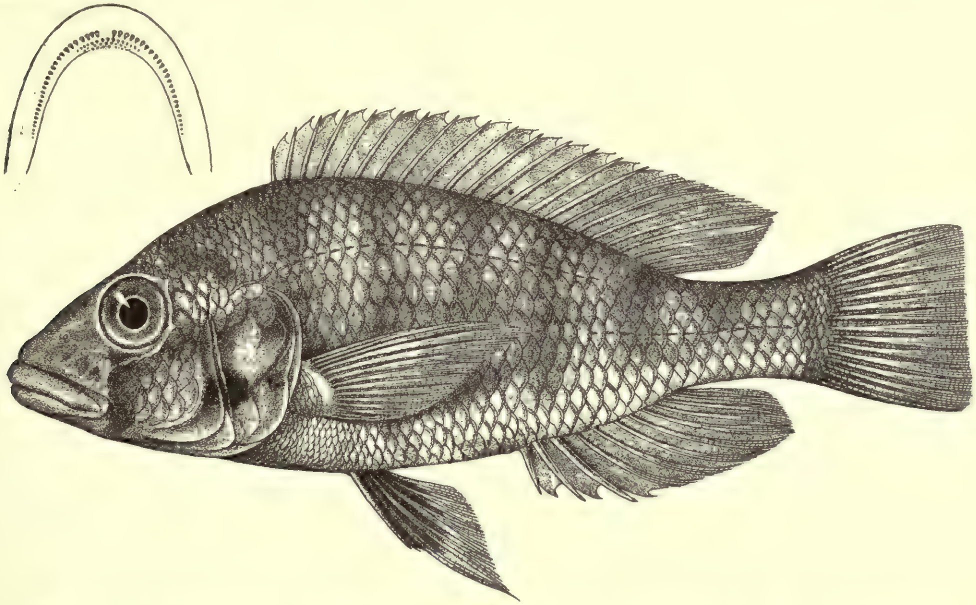

FIG. 13. *Haplochromis riponianus*; lectotype (from Boulenger, *Ann. Mus. Genova*).

Mouth horizontal or very slightly oblique, jaws equal anteriorly, the lower 33·4–42·2 (M = 38·5) per cent of head and 1·3–2·0 (modal range 1·6–1·8) times as long as broad. Posterior tip of the maxilla extending to the vertical through the anterior orbital margin or almost so, occasionally to below the anterior quarter of the eye. Lips noticeably thickened but not produced into median lobes.

Gill rakers on the first arch moderately stout in most fishes but slender in a few others, the lowermost one to three reduced and the pair nearest the epi-ceratobranchial angle often flattened and tri- or quadrifid; 6–8 (mode 7) rakers on the lower part of the arch.

Scales ctenoid; lateral line with 30 (f.2), 31 (f.2), 32 (f.11), 33 (f.10) or 34 (f.2) scales, cheek with 3 or 4 series; 5½-7 (rarely 5 or 8) scales between the lateral line and the dorsal fin origin; 7 or 8 (rarely 6) between the pectoral and pelvic fin bases. Scales on the pectoral region moderate.

Fins. Dorsal with 24 (f.3), 25 (f.24) or 26 (f.1) rays, anal with 11 (f.3) or 12 (f.25), comprising XV–XVI, 9–10 and III, 8 or 9 spinous and branched rays for the fins respectively. Pectoral 69·0–88·5 (M = 78·5) per cent of head. Caudal sub-truncate.

Teeth. The outer teeth in both jaws are relatively slender and slightly to strongly recurved ; the basic cusp pattern is unequally bicuspid, but the crowns are often so worn that the teeth appear to be weakly cuspidate or even unicuspid and bluntly incisiform. In some fishes over 80 mm. S.L. initially unicuspid teeth occur and may even be the predominating form in fishes more than 100 mm. S.L. The number of teeth in the upper, outer rows shows slight positive allometry with standard length ; there are 38–62 teeth in this row.

Unicuspid and weakly tricuspid teeth are found in the inner rows ; often both types of teeth occur together, especially in fishes over 80 mm. S.L. The inner teeth are implanted at an angle and may be buried in the thickened oral mucosa (possibly a preservation artefact). In the upper jaw, the inner teeth are arranged in 3 or 4 (rarely 2) rows and in the lower in 2–4 (rarely 1) rows.

Boulenger's description (1911 and 1915) of the inner teeth as " minute " appears to stem from his being misled by the thickened oral epithelium which has hidden all but the tips of these teeth.

Lower pharyngeal bone and teeth. The lower pharyngeal bone is triangular and in most specimens fairly stout. The relative degree to which the bone is enlarged is somewhat greater than that of the lower pharyngeal in *H. humilior* (see p. 250). In a few fishes, however, the bone is slender. This variation in stoutness is not entirely correlated with size since, although the smallest specimens have slender or but slightly thickened bones, some of the larger fishes do not have proportionately enlarged pharyngeals.

The form of the teeth in the four median rows does show correlation with both the size of the individual and the stoutness of the bone. In fishes less than *ca.* 70 mm. S.L. some of the posterior teeth in the two median rows are enlarged ; in fishes 70–80 mm. most of the median teeth are enlarged as are some or all of the teeth in the row on each side of the two median rows. Next, in specimens above 80 mm. S.L. (except those with slender pharyngeal bones) the teeth of these four rows are larger still, whilst those in the two median rows tend to be molariform. Finally, in fishes over 98 mm. S.L. some of the more lateral teeth are also molariform. Large individuals with slender lower pharyngeals have only slightly enlarged median teeth, comparable with those of the smaller (< 90 mm.) specimens described above.

Osteology. The shape of the neurocranium departs from the generalized type towards the form found in the elongated, piscivorous predators (as typified by *H. mento*). In *H. riponianus*, the slope from the anterior tip of the vomer to the base of the supraoccipital crest is less steep and more nearly straight than in the generalized type of skull ; also, the preorbital region in *H. riponianus* is relatively longer than in, for example, the skull of *H. obliquidens* or *H. macrops*.

Coloration. The colours of live fishes are unknown.

Preserved material. Sexually active males. Ground colour greyish-brown, chest dusky ; a dark lachrymal stripe and faint traces of four interrupted transverse bars on the flanks. Dorsal, caudal and anal fins hyaline, the anal with two or three dead-white ocelli, usually arranged in a single row, but occasionally in two rows. Pelvic fins black. *Immature males* similar to females but with darker pelvics and small, distinct ocelli on the anal fin. *Females* silvery-grey shading to silver ventrally; six to ten transverse bars of variable width (narrowest when most numerous) across the flanks and caudal peduncle; sometimes, a very faint lachrymal stripe. All fins hyaline, the caudal occasionally maculate; in a few specimens there are one or two, small, dead-white spots in the same position as the ocelli on the anal fin of males.

Distribution. Lake Victoria and possibly the Victoria Nile. The latter locality is surmised from the data given in the original description of the species. In that paper (Boulenger, 1911), the locality is given only as Jinja, Ripon Falls, but in the introduction Boulenger implies that the entire collection, of which *H. riponianus* formed part, was from the Victoria Nile, that is *below* the Ripon Falls. Later (*Cat. Afr. Fish.* **3**, 1914) the type locality is given more specifically as " Ripon Falls, Victoria Nile."

Ecology. Habitat. The species is apparently confined to sand or rock substrates in the littoral regions of the lake; it has been caught in both exposed and sheltered localities.

Food. Stomach and intestinal contents of thirty-two fishes (from one locality) show that at least this population of *H. riponianus* was mainly insectivorous, although some fishes had also fed on Mollusca. Insect larvae (especially Trichoptera and Ephemeroptera) were found in every fish. As in *H. humilior* (see p. 251) large quantities of uniformly sized sand-grains were found in the intestines of most fishes. Since these grains closely resemble those forming the cases of certain Caddis-fly larvae found intact in some individuals, it is suggested that the sand was derived, at least partly, from crushed cases. In addition to the main contents listed above, eight fishes contained relatively large quantities of crushed bivalve shells (? *Corbicula* sp.); a few fragments of gastropod shells were also found in these individuals.

Breeding. No information is available on the breeding habits of *H. riponianus*. The smallest sexually mature fish is a female 84 mm. S.L.; the smallest adult male is 86 mm. S.L.

Affinities. In combination, the oral and pharyngeal dentition set *H. riponianus* apart from other Lake Victoria species. In appearance and in possessing a similar oral dentition, *H. saxicola* (see p. 257) appears to be the nearest relative of *H. riponianus* although it differs in having a relatively slender pharyngeal bone with only the two median tooth rows slightly enlarged. The two species, which differ somewhat in their ecological relationships, may represent separate adaptive lines derived from a common ancestor.

Haplochromis pallidus seems structurally suited for consideration as the extant representative of the presumed ancestor. (See also p. 235.)

Although the lower pharyngeal bone and its dentition are similar in *H. humilior* and *H. riponianus* and although both species have very similar ecological requirements, the species show quite marked divergence in body-form (especially head shape) and oral dentition. What relationships there are probably lie far back in their phylogenetic history; certainly the two species cannot be considered members of a recently evolved phyletic line.

Boulenger's view (1911) that *H. riponianus* and *H. microdon* are closely related can no longer be held; the two species have very different phylogenies, as witnessed by several anatomical and osteological characters, and equally distinctive habits (Greenwood, 1959). Boulenger was undoubtedly misled by the supposedly small teeth of both species (Greenwood, op. cit., and above) whereas in fact the teeth of *H. riponianus* are not minute and are of a markedly different form from those of *H. microdon*.

Study material and distribution records

Museum and Reg. No.		Locality	Collector
		Uganda	
Genoa Museum (C.E. 12996 (Lectotype)		Jinja, Ripon Falls	Bayon
B.M. (N.H.)	1911.3.3.37–39	,, ,,	,,
,,	1911.3.3.24	,, ,,	,,
,,	1906.5.30.280	Entebbe	Degen
,,	1906.5.30.394 (Paratype *H. ishmaeli*)	Bunjako	,,
,,	1929.8.13.1	Entebbe	Hoare
,,	1959.4.28.141–157	Entebbe, Airport beach	E.A.F.R.O.
,,	1959.4.28.158	Hannington Bay	,,
,,	1959.4.28.159	Buka Bay	,,
,,	1959.4.28.160–162	Entebbe, Harbour	,,
		Lake Victoria, Locality Unknown	
,,	1901.6.24.86–87	—	Sir H. Johnson
,,	1928.5.24.136–138	—	M. Graham

Haplochromis saxicola, sp. nov.

(Text-figs. 5 and 14)

Pelmatochromis riponianus (part) Boulenger, 1911, *Ann. Mus. Genova* (3), **5**, 69; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 411.

Haplochromis cinereus (part) Regan, 1922, *Proc. zool. Soc. London*, 166.

Holotype. A female 111·0 + 25·0 mm. long (B.M. (N.H.) Reg. No. 1959.4.28.249) from Ramafuta island, Uganda.

Description, based on twenty-seven specimens (including the holotype of the species and two paratypes of *Pelmatochromis riponianus*) 106–123 mm. S.L.

Depth of body 34·8–42·5 (M = 37·8) per cent of standard length, length of head 35·3–42·5 (M = 37·8) per cent. Dorsal head profile straight or gently curved, sloping at *ca.* 30°–40°. Preorbital depth 15·2–19·0 (M = 17·6) per cent of head, least interorbital width 23·9–29·8 (M = 26·9) per cent. Snout slightly longer than broad or, less commonly, as long as broad, its length 34·0–41·8 (M = 37·5) per cent of head ; diameter of eye 20·4–26·8 (M = 24·4), depth of cheek 21·4–26·2 (M = 23·9) per cent. Caudal peduncle 13·1–17·7 (M = 15·4) per cent of standard length, 1·0–1·5 (mode 1·3) times as long as deep.

Mouth horizontal or very slightly oblique ; lips variably thickened but always noticeably enlarged. Lower jaw 39·7–46·5 (M = 43·0) per cent of head and 1·5–1·9 (mode 1·8) times as long as broad. Posterior tip of the maxilla reaching or almost reaching the vertical through the anterior orbital margin, sometimes extending to below the eye.

Gill rakers moderately stout, the uppermost two or three either slender or divided and somewhat flattened, the lowermost one to three usually reduced ; 7–9 (mode 8) rarely 6 on the lower part of the first arch.

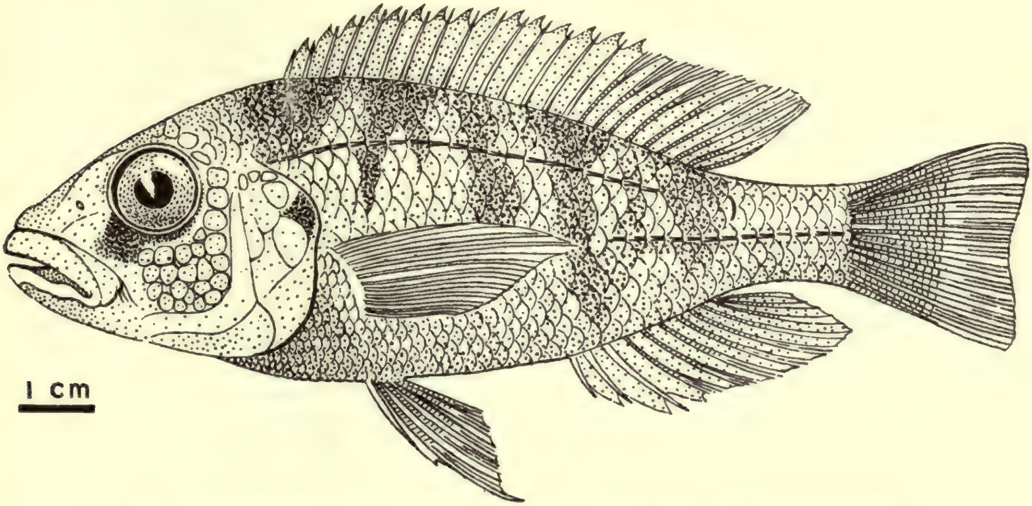

FIG. 14. *Haplochromis saxicola ;* holotype. Drawn by John Norris Wood.

Scales ctenoid ; 31 (f.2), 32 (f.15), 33 (f.9) or 34 (f.1) in the lateral line ; cheek with 3 or 4 series. Six or 7 (rarely 5) between the lateral line and the dorsal fin origin ; 6–8 (rarely 5 or 9) between the pectoral and pelvic fin bases. Scales on the pectoral region small.

Fins. Dorsal with 24 (f.4), 25 (f.20) or 26 (f.2) rays, anal with 11 (f.1), 12 (f.24) or 13 (f.1), comprising XIV–XVI, 9 or 10 and III, 8–10 spinous and branched rays for the fins respectively. One specimen has XVI, 6 rays in the dorsal and another II, 8 in the anal. Pectoral 67·8–81·0 (M = 74·5) per cent of head. Caudal truncate or sub-truncate.

Teeth. In the outer series of each jaw the teeth are slender, recurved and generally unicuspid, but a few weakly bicuspid teeth may occur in fishes less than 115 mm. S.L.

The crowns of the teeth are often worn so as to assume a bluntly incisiform shape. There are 52–68 teeth in the outer row of the upper jaw (modal range 60–62).

The inner tooth rows are composed of obliquely implanted and either unicuspid or both uni- and tricuspid teeth arranged in 2 or 3 (rarely 4 or 5) rows in each jaw.

The dentition of *H. saxicola* bears a very strong resemblance to that of *H. riponianus,* the major difference lying in the higher percentage of primarily unicuspid teeth in *H. saxicola.* However, it must be borne in mind that no available specimens of *H. riponianus* are as large as even the smallest *H. saxicola.*

Lower pharyngeal bone and teeth. In ninety per cent of specimens examined, the lower pharyngeal bone is not enlarged ; in the remaining ten per cent it is somewhat thickened and resembles the lower pharyngeal of *H. riponianus.*

The two median tooth rows are slightly enlarged in all specimens and may even be molariform in those individuals with enlarged lower pharyngeal bones. Very exceptionally, the median teeth are not noticeably larger than the more lateral ones.

Osteology. The neurocranium of *H. saxicola* is very like that of *H. riponianus* (see p. 254) ; the premaxilla is, however, distinctive for its noticeably arched dentigerous arms which impart a characteristic peak to the antero-medial part of the bone.

Coloration in life. Sexually active males. Ground colour dark grey-green, some scales on the flank with golden centres ; chest and branchiostegal membrane black ; a coppery-red flush on the operculum and flanks. Dorsal fin dark, lappets and maculae red ; caudal blue-grey with red posterior and ventral margins ; anal fin blue-grey, suffused with pink, especially the distal margins, ocelli bright yellow ; pelvic fins black. *Quiescent males* pale silvery-blue, almost grey dorsally ; some flank scales with golden centres, pectoral region silver. Dorsal, caudal and pelvic fins hyaline, the dorsal with pale red lappets and margin to the soft part, pelvics dusky on the lateral half, hyaline mesially. *Females.* Ground colour golden-grey ; all fins hyaline.

Preserved material. Adult males (probably sexually active). Ground coloration dark grey-black, especially dark on the head, dorsal aspects of the flanks and along the ventral body surface. Lips light grey ; branchiostegal membrane black. Dorsal fin dark, with light maculae on the soft part. Anal fin black on the basal third, the distal two-thirds yellowish, with two grey ocelli. Caudal greyish ventrally, yellow around the margin.

Females, juvenile and some apparently adult (*? quiescent*) *males.* Brownish-yellow ground coloration, darkest on the dorsal surface of the head ; four to seven, fairly narrow dark transverse bars on the flanks and caudal peduncle. Dorsal and caudal fins greyish, all other fins colourless, except for the black pelvics in adult males.

Distribution. The species is known definitely from Lake Victoria but may also occur in the Victoria Nile. This locality is suggested by the presumed provenance of two *P. riponianus* paratypes now considered to be *H. saxicola.* For further discussion, see under " Distribution " in *H. riponianus,* p. 255.

Ecology. Habitat. The habitats in which *H. saxicola* has been caught are rather more varied than is common for most Lake Victoria *Haplochromis.* The species occurs in shallow water over exposed sand or shingle beaches, amongst dense plant stands near rocky shores and over shingle and small boulders in water 10–30 feet deep. Finally, one specimen was caught more than a mile off-shore in nets set on a mud bottom in water *ca.* 180 feet deep. The most consistent factors in all these habitats (except the latter) are the hard substrates of sand, rock or shingle.

Food. Twenty-six fishes (from nine different localities) were examined ; of these, only twelve contained any ingested material in the stomach or intestine. Sand grains and small pebbles (*ca.* 2 mm. in diameter) were found in eleven individuals ; fragmentary insect larvae (Diptera, probably chironomids) formed the principal food in eight fishes and snails in one other. All specimens contained a few fragmentary Ostracoda and one, an almost entire larva of the boring May-fly *Povilla adusta.*

These very unsatisfactory data suggest that *H. saxicola* is a bottom feeder which preys on various invertebrates, particularly insect larvae.

Breeding. No information was obtained on the breeding habits of *H. saxicola* ; the smallest specimen (106 mm. S.L.) is sexually mature. Both sexes appear to reach the same maximum adult size.

Affinities. In general appearance, oral dentition, neurocranial morphology and in certain ecological characters, *Haplochromis saxicola* closely resembles *H. riponianus.* The most striking difference between the species is the typically slender lower pharyngeal bone of *H. saxicola* and the stouter pharyngeal bone and teeth of *H. riponianus.* The mean snout and lower jaw proportional lengths for *H. saxicola* are somewhat greater than those for *H. riponianus.* If, however, these characters are taken for both species and plotted against standard length, no marked discontinuity is observed ; in all morphometric characters *H. saxicola* could well be large *H. riponianus.*

The differences in the lower pharyngeal bones and dentition, however, are against this interpretation, the more slender bone with but slightly enlarged median teeth characterizing the larger specimens described as *H. saxicola.* In no *Haplochromis* species with enlarged pharyngeals does the bone and its dentition become less coarse with growth. Indeed, the reverse is usual (see Greenwood, 1959 and p. 277).

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1959.4.28.249 (Holotype)	Ramafuta Isl.	E.A.F.R.O.
,, 1911.3.3.39 (Paratype of *Pelmatochromis riponianus*)	Jinja, Ripon Falls	Bayon
Genoa Museum (A paratype of *P. riponianus*)	,, ,,	Bayon
B.M. (N.H.).—1959.4.28.250–255	Ramafuta Island	E.A.F.R.O.
,, 1959.4.28.256–267	,, ,,	,,
,, 1959.4.28.268–270	Beach near Nasu Point	,,
,, 1959.4.28.271–272	Jinja	,,
,, 1959.4.28.273	0° 4′ S., 33° 14′ E.	,,

Haplochromis theliodon sp. nov.

(Text-figs. 12 and 15)

Holotype. A fish 95·0 + 20·0 mm. long (B.M. (N.H.) Reg. No. 1959.4.28.163) from Majita, Tanganyika Territory.

Description, based on seven specimens (including the holotype) 79–95 mm. S.L. The principle morphometric characters are summarized below:

S.L.	Depth*	Head*	Po. %	Io. %	Snt. %	Eye %	Ck. %	L.j. %	C.P.*
75·0	37·3	37·3	17·9	25·0	32·2	25·0	21·4	39·3	15·3
84·0	35·7	36·9	16·2	25·8	32·2	26·8	25·8	38·7	14·3
85·0	36·6	36·6	16·1	22·6	35·5	24·2	22·6	38·7	15·4
86·0	38·4	33·7	17·3	24·1	33·5	24·1	24·1	38·0	15·1
88·0	38·6	36·3	18·1	25·0	34·4	25·0	24·4	37·4	14·8
89·0	38·2	36·5	18·5	24·6	33·8	24·6	27·0	38·4	15·2
95·0	36·8	33·7	17·2	25·0	34·4	26·6	25·0	39·0	13·7

* Per cent. of standard length.
% Per cent. of head length.

Dorsal head profile straight except for a slight concavity above the eye, sloping fairly steeply; snout longer than broad. Mouth slightly oblique; lips, especially the upper, thickened. Lower jaw 1·5–1·8 times as long as broad. Posterior tip of the maxilla almost reaching the vertical to the anterior orbital margin.

Gill rakers variable, from stout (the commonest) to relatively slender; 7 (f.1), 8 (f.5) or 9 (f.1) on the lower part of the first arch. The lowermost two to four rakers may be reduced.

Scales ctenoid; lateral line with 31 (f.2), 32 (f.3) or 33 (f.2) scales; cheek with 3 or 4 series. Six to 9 scales between the lateral line and the dorsal fin origin, 7–9 between the bases of the pectoral and pelvic fins. Scales on the pectoral region small and deeply embedded.

Fins. Dorsal with 25 rays, anal with 12, comprising XV–XVI, 9 or 10 and III, 9 spinous and branched rays for the fins respectively. Pectoral 64·3–72·0 (M = 69·5) per cent of head. Caudal truncate or sub-truncate.

Teeth. In six of the seven specimens examined, the outer row in both jaws is composed of relatively stout, unequally bicuspid teeth, except for the most posterior pair in the upper jaw which are unicuspid. In the seventh specimen, the anterior and postero-lateral teeth are unicuspid and the lateral teeth unequally bicuspid. There are 36–46 outer teeth in the upper jaw.

The inner teeth are small and tricuspid (with a few unicuspids in the exceptional specimen mentioned above) and are arranged in 3 or 4 rows in the upper jaw and 3 or 4 (rarely 2) in the lower. Inner teeth are implanted vertically or somewhat obliquely.

Lower pharyngeal bone and teeth. The lower pharyngeal bone is thickened and moderately stout; that is to say, it is comparable with the lower pharyngeal in most *H. humilior* but finer than that in *H. obtusidens* (see p. 267).

Five of the seven specimens examined have the four median tooth rows composed of large and molariform teeth, whilst the next lateral row of each side contains enlarged but clearly cuspidate teeth. In the exceptional fishes, only the median pair of tooth rows contains molariform elements and only one lateral row on each side has enlarged teeth.

Coloration. The colours of live fishes are unknown.

Preserved material. Quiescent male. Ground colour dusky bronze, with a very faint mid-lateral stripe, six interrupted transverse bars and a distinct lachrymal stripe. Dorsal fin dark, lappets pale ; caudal dark except for its pale distal margin ; anal pale (? orange) with four, small, white ocelli arranged in a single row. Pelvics black on the outer two-thirds, lighter medially. *Females and immature males* uniformly light brown except for the darker dorsal head surface and nape ; a dark mid-lateral stripe of variable intensity is continuous in some specimens but interrupted in others above and slightly anterior to the anal fin ; when interrupted, the line is thickened to form a black blotch above the pectoral fin. A fainter, continuous dorsal stripe runs above the upper lateral line ; there are traces of seven to nine, variously interrupted transverse bars on the flanks but not on the caudal peduncle. Dorsal and anal fins hyaline, darker between the branched rays. Caudal maculate on the upper half, immaculate below. Pelvic fins hyaline in females but with the outer half dusky in males.

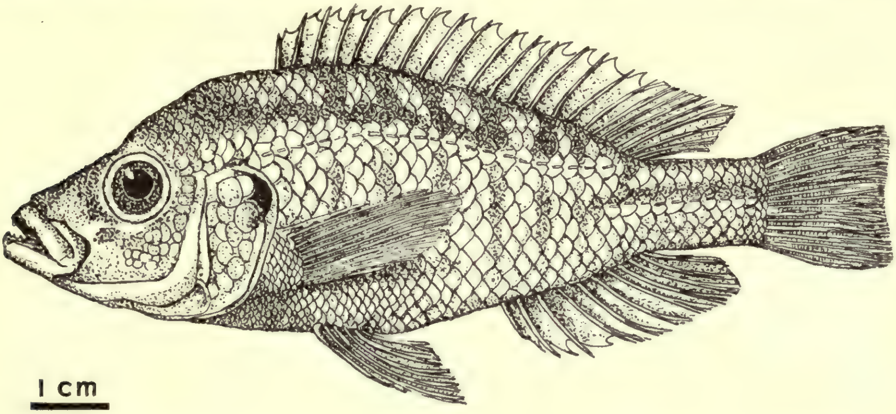

FIG. 15. *Haplochromis theliodon ;* holotype. Drawn by Miss G. Osterritter.

Distribution. Known only from Lake Victoria.

Ecology. Habitat. The few specimens known came from two localities, both exposed, shallow and sandy beaches.

Food. Analysis of stomach and intestinal contents from all seven specimens indicate that *H. theliodon* is a bottom feeder with a varied diet including small fishes (cichlids, 20–25 mm. long), Gastropoda (foot and soft parts only), Lamellibranchiata and insect larvae, e.g. *Povilla adusta* (Ephemeroptera) and Trichoptera (including the cases). Each fish had also ingested fairly large quantities of bottom debris.

Breeding. Few data are available; one female 75 mm. S.L. is sexually mature whilst another, 88 mm. S.L. appears to be a juvenile maturing for the first time.

Diagnosis and affinities. The nature of its lower pharyngeal bone and dentition places *H. theliodon* on the same level of structural modification as *H. humilior* and *H. riponianus*. In other characters (especially general appearance and oral dentition) *H. theliodon* is unlike both the former species. It differs from *H. humilior* in several morphometric characters (straight and not curved dorsal head profile, deeper preorbital, longer snout and smaller eye) and from *H. riponianus* in the shape of the head and the nature of its oral dentition. *Haplochromis theliodon* also differs from both the other species in having much smaller and more deeply embedded pectoral scales.

The affinities of *H. theliodon* are not easily determined except in so far as the species is clearly a little-modified derivative of the generalized stem. The small pectoral scales of *H. theliodon* are not common in generalized species still extant in Lake Victoria; but, small chest scales do characterize certain of the generalized and fluviatile species of East Africa, some of which also show an incipient hypertrophy of the pharyngeal bones and dentition (Greenwood, unpublished).

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Tanganyika	
B.M. (N.H.).—1959.4.28.163 (Holotype)	Majita	E.A.F.R.O.
,, 1959.4.28.164–168	,,	,,
	Uganda	
,, 1959.4.28.169	Jinja Pier	,,

Haplochromis empodisma sp. nov.

(Text-figs. 16 and 17)

Haplochromis ishmaeli (part) Boulenger, 1906, *Ann. Mag. nat. Hist.* (7), **17**, 446; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 293; Regan, 1922, *Proc. zool. Soc. London*, 169.
Tilapia lacrimosa (part), Boulenger 1906, *op. cit.*, 450; *Idem*, 1915, *tom. cit.*, 234.
Haplochromis cinereus (part) Regan, 1922, *op. cit.*, 166.

Note. Because two specimens of *H. empodisma* (collected during Graham's 1927–28 survey of Lake Victoria) were mistaken for syntypes of *H. michaeli* Trewavas, this species was referred to as *H. michaeli* in previous papers (Greenwood, 1954, 1956*a*). All references to "*H. michaeli*" in these publications should now be corrected to read *Haplochromis empodisma*.

Holotype. An adult male 117 + 23 mm. total length (B.M. (N.H.) Reg. No.

1959.4.28.170), caught on the bottom in 90 feet of water off the southern tip of Kibibi Island (0° 10′ N.; 33° 10′ E.), Uganda.

Description, based on thirty-nine fishes (including the holotype) 65–117 mm. S.L.

Depth of body 33·0–43·8 (M = 39·3) per cent of standard length, length of head 33·3–39·4 (M = 36·7) per cent. Dorsal head profile straight or gently curved, sloping at an angle of 35°–40°. Preorbital depth 15·1–20·5 (M = 18·1) per cent of head; least interorbital width 20·6–28·6 (M = 24·3), length of snout 27·5–37·2 (M = 32·9), diameter of eye 24·4–34·0 (M = 27·3) per cent. Depth of cheek shows a marked positive allometry with standard length, being 21·2–23·0 per cent of head in fishes less than 80 mm. S.L. (N = 4) and 23·5–31·4 (M = 27·9) per cent in larger specimens (N = 35). Caudal peduncle 14·5–20·0 per cent of standard length and 1·3–1·7 (mode 1·4) times as long as deep.

Mouth horizontal or slightly oblique; lips not noticeably thickened. Posterior tip of the maxilla reaching the vertical through the anterior margin of the orbit or to below the anterior part of the eye; less frequently, not reaching as far as the orbit. Lower jaw 39·1–48·7 (M = 43·9) per cent of head, 1·5–2·3 (mode, ill-defined, 2·0) times as long as broad. Malformation of the lower jaw is relatively common in this species; individuals so affected have the lower jaw broader than the upper (which closes within the lower) and are distinctly prognathous.

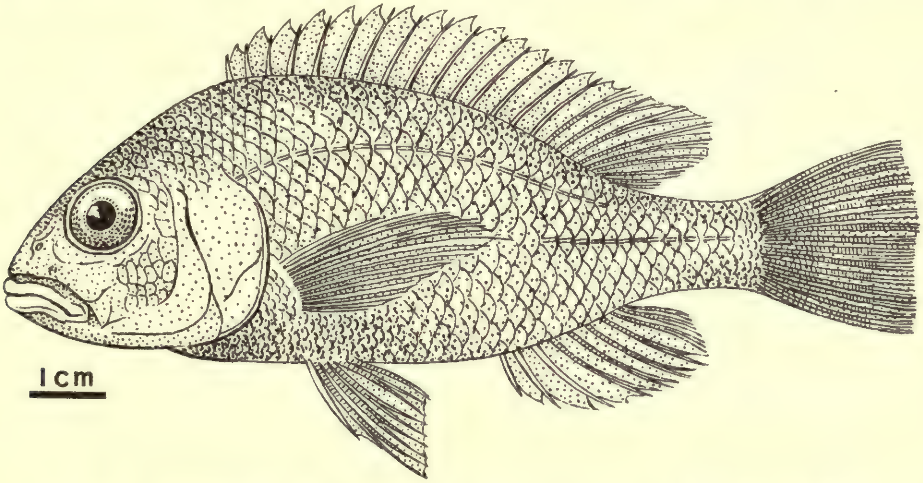

FIG. 16. *Haplochromis empodisma*; holotype. Drawn by John Norris Wood.

Gill rakers usually slender, although relatively stout rakers also occur; 7–10 (modal range 8–9) on the lower part of the first gill arch, the lowermost 1–3 rakers reduced, occasionally the uppermost 1 or 2 somewhat flattened and bi- or trifid.

Scales ctenoid; lateral line with 30 (f.10), 31 (f.9), 32 (f.15) or 33 (f.4) scales. Cheek with 3 or 4 (occasionally 5) series. Six or 7 scales between the lateral line and the dorsal fin origin, 6–8 between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.8), 24 (f.30) or 25 (f.1) rays, anal with 10 (f.1), 11 (f.22) or 12 (f.16), comprising XIV–XVI, 8 or 9 and III, 7–9 spinous and branched rays for the fins respectively. Pectoral fin 73·0–96·5 (M = 85·8) per cent of head. Caudal truncate or sub-truncate.

Teeth. The teeth in the outer row of both jaws are slender and often gently recurved ; in fishes less than 95 mm. S.L. the teeth are unequally bicuspid but in larger individuals are weakly bicuspid or unicuspid ; it is usual to find both types of teeth in large fishes. There are 54–82 (modal range 70–72) teeth in the upper jaw.

Teeth forming the inner series are small and usually tricuspid but some unicuspids may occur, particularly in fishes over 100 mm. S.L. ; there are 2 or 3 (rarely 4) rows in the upper jaw and 1–3 in the lower. The innermost row, especially in the upper jaw, is implanted obliquely.

A common abnormality affecting both inner and outer teeth is for the crowns to be coarse, slightly swollen and darkly pigmented ; in such teeth the crown is globose.

Lower pharyngeal bone and teeth. The lower pharyngeal is fine and rather narrow, the dentigerous surface having the outline of an isosceles triangle. Usually, none of the pharyngeal teeth is markedly enlarged, but in certain specimens of all sizes a few teeth in the two median rows are slightly coarser. Even when enlarged these teeth retain the same form as their lateral and more slender congeners.

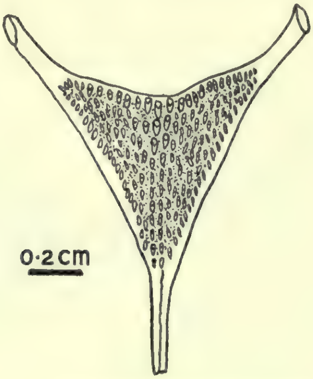

FIG. 17. *Haplochromis empodisma ;* lower pharyngeal bone, occlusal view.

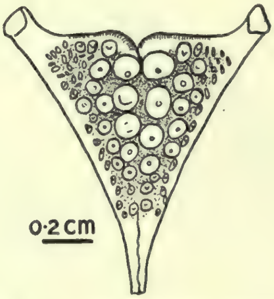

FIG. 18. *Haplochromis obtusidens ;* lower pharyngeal bone, occlusal view.

Osteology. The neurocranium and dentary of *H. empodisma* were figured and briefly described in an earlier paper (Greenwood, 1956*a*, p. 305, fig. 5 ; the species was then wrongly identified as *H. michaeli*). Both the neurocranium and the jaw elements are directly comparable with those of a generalized species such as *H. macrops*, except that in *H. empodisma* the outer teeth are more numerous.

Coloration in life. Sexually active males. Ground colour dark turquoise on the flanks and dorsal body surface, silver-yellow ventrally ; snout and dorsal head surface dark red. Dorsal and caudal fins diffuse red ; anal black anteriorly, dark red posteriorly, the ocelli orange-red. Pelvic fins black. *Quiescent males* as for females (see below) but dorsal fin with red maculae between the branched rays. Ripening males show some reddening of the head and snout, whilst the maculae of the dorsal are more intense. *Females.* Ground colour yellowish-silver, darker dorsally. Dorsal and caudal fins dark neutral; anal yellow; pelvics very pale yellow.

Preserved material. Males (sexually active), dark grey becoming black ventrally; a distinct lachrymal stripe and two bars across the snout (quiescent males greyish brown, dusky on the belly; very faint indications of up to five incomplete transverse bars on the flanks; lachrymal stripe visible but no bars across the snout). Dorsal fin dark, the lappets black; caudal dark proximally, lighter distally; basal third of anal black, remainder of fin light, with two or three large white ocelli. Pelvic fins black. *Females* brownish-silver; in a few specimens there are very faint indications of a lachrymal stripe and of incomplete transverse bars on the flanks. All fins hyaline; in some fishes the upper half of the caudal is slightly maculate.

Distribution. Known only from Lake Victoria.

Ecology. Habitat. It seems that *H. empodisma* is generally restricted to those areas of the lake where the bottom is composed of organic mud. The species has been caught in bottom nets set at depths from 10–90 feet.

Food. The stomach and intestinal contents of thirty-seven fishes (from numerous localities) show that *H. empodisma* is a bottom feeder. The principal food organisms are the larval (and less frequently pupal) stages of dipterous insects, together with diatoms derived from the bottom mud. Only two fishes yielded remains of Mollusca; in one fish a few fragments of bivalve shell were found and in the other an operculum from a large gastropod. Since no other snail fragments were found in this fish, it is possible that the operculum was accidentally ingested.

Breeding. It is not known whether *H. empodisma* spawns in the habitats described above or whether spawning takes place over a more solid substrate, for example outcrops of rock or sand. Females carrying embryos and larvae have been caught together with non-breeding fishes. The smallest sexually active fish is a female 84 mm. S.L.; the smallest adult male is 90 mm. S.L. Both sexes reach the same maximum adult size.

Affinities. Structurally and in its feeding habits, *H. empodisma* must be considered a generalized species. It differs from the majority of generalized forms in Lake Victoria only by its larger size, greater number of teeth (possibly a correlate of the larger size) and in the wide range of depths at which it has been caught. The nearest living relative of *H. empodisma* is a small and as yet undescribed species which occurs in the same habitat but is confined to shallow water.

Haplochromis empodisma and *H. obtusidens* are strikingly similar except for one structure, the lower pharyngeal bone. In *H. obtusidens* the lower pharyngeal is thickened and carries a number of enlarged, crushing teeth, whereas in *H. empodisma* this bone is slender and carries numerous fine teeth. *Haplochromis empodisma* could well represent the ancestral type from which *H. obtusidens* was derived by an increase in size of the pharyngeal bones and a correlated change in the pharyngeal dentition. Although the inter-specific differences in the nature of the pharyngeal mill are fairly clear-cut, some individuals deviate from the specific mode in such a way as to indicate a likely transitional condition in the evolution of an "*obtusidens*"-like species.

Since, in turn, *H. obtusidens* provides a structural type basic to the evolution of a specialized crushing pharyngeal mill (as found in *H. ishmaeli* and *H. pharyngomylus*), *H. empodisma* could represent the extant representative of the basal species in the phyletic line which culminated in *H. ishmaeli* and *H. pharyngomylus*.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1959.4.28.170 (Holotype)	Off Kibibi Island	E.A.F.R.O.
,, 1906.5.30.472	Entebbe	Degen
,, 1906.5.30.402 (Paratype, *H. ishmaeli*)	Bunjako	,,
,, 1906.5.30.404 (Paratype, *H. ishmaeli*)	,,	,,
,, 1959.4.28.180–189	Pilkington Bay	E.A.F.R.O.
,, 1959.4.28.194–195	Thruston Bay	,,
,, 1959.4.28.196–197	Ekunu Bay	,,
,, 1959.4.28.198	Jinja	,,
,, 1959.4.28.199	Napoleon Gulf, near Jinja	,,
,, 1959.4.28.202–203	Kibibi Island	,,
,, 1959.4.28.358	Off S. tip of Kibibi Island	,,
	Tanganyika	
,, 1959.4.28.190–193	Nyamakyamwa	E.A.F.R.O.
	Kenya	
,, 1959.4.28.200–201	Manadu Island	,,
,, 1959.4.28.171–179	Off Port Southby	,,
	Lake Victoria, Locality Unknown	
,, 1928.6.2.37–38	—	M. Graham

Haplochromis obtusidens Trewavas 1928

(Text-fig. 18)

Haplochromis desfontainesi (part), Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 302.
Tilapia lacrimosa (part), Boulenger, 1915, *tom. cit.*, 234.
Haplochromis cinereus, (part) Regan, 1922, *Proc. zool. Soc. London*, 166.
Haplochromis obtusidens Trewavas, 1928, *Ann. Mag. nat. Hist.* (10), **2**, 95.

Lectotype. An adult male 107·0 + 23·0 mm. total length (B.M. (N.H.) Reg. No. 1928.5.30.21).

Description, based on forty-four specimens (including the lectotype and one paratype) 60–114 mm. S.L.

Certain proportions show fairly well-marked allometry with standard length ; for these, ranges and means are given for each of the relevant size-groups.

Depth of body 35·0–44·3 (M = 38·6) per cent of standard length, length of head 32·5–38·2 (M = 35·8) per cent. Dorsal head profile gently curved or, less commonly, straight, sloping at an angle of 40°–50°. Preorbital depth in fishes < 70 mm. S.L.

(N = 4), 13·0–16·7 (M = 14·5) per cent of head, in larger fishes (N = 40) 15·1–20·5 (M = 17·9); least interorbital width 21·8–29·0 (M = 24·2) per cent; snout length in fishes < 85 mm. S.L. (N = 6), 26·0–31·0 (M = 28·5) per cent, in larger individuals (N = 38), 29·0–36·4 (M = 33·3); diameter of eye in fishes < 85 mm., 27·6–34·8 (M = 31·2) per cent and in larger fishes 24·3–30·8 (M = 27·2); depth of cheek in specimens < 85 mm., 18·6–23·8 (M = 21·5) and in larger individuals 21·2–30·0 (M = 26·7) per cent of head. Caudal peduncle 15·2–19·7 (M = 17·5) per cent of standard length, 1·2–1·8 (mode 1·5) times as long as deep.

Jaws equal anteriorly; mouth horizontal or slightly oblique; lips not markedly thickened. Posterior tip of the maxilla extending to the vertical through the anterior orbital margin or to below the anterior part of the eye; exceptionally, not reaching the orbit. Lower jaw 37·9–45·5 (M = 41·8) per cent of head and 1·3–2·0 (mode 1·6) times as long as broad.

Gill rakers relatively slender, although short and stout rakers are found in a few individuals; 7–9 (modal range 7–8), rarely 6, on the lower part of the first arch, the upper pair of rakers often flattened.

Scales ctenoid; 29 (f.1), 30 (f.7), 31 (f.21), 32 (f.11) or 33 (f.4) in the lateral line; cheek with 3 or 4 (rarely 5) series; 5½–7 scales between the lateral line and the dorsal fin origin, 5–7 (rarely 9) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.13), 24 (f.25) or 25 (f.6) rays, anal with 11 (f.24), 12 (f.19) or 13 (f.1), comprising XIV–XVI, 8–10 and III, 8–10 spinous and branched rays for the fins respectively. Pectoral 73·5–103·0 (M = 86·8) per cent of head. Caudal truncate or sub-truncate.

Teeth. In fishes less than 90 mm. S.L., the outer row in both jaws is composed of unequally bicuspid and relatively slender teeth. Larger individuals have an admixture of either unequally bicuspid and unicuspid teeth or of weakly bi- and unicuspids. A few individuals have exclusively bicuspid or unicuspid teeth. There are 40–80 teeth (ill-defined mode at 70; modal range 66–70) in the outer row of the upper jaw.

Teeth in the inner series are generally tricuspid and small; in some fishes over 100 mm. S.L. there may be either a mixture of tri- and unicuspid teeth or, more rarely, only unicuspids. The innermost row of teeth (especially in the upper jaw) is implanted obliquely and in some individuals the whole inner series lie at an oblique angle. There are 2 or 3 (rarely 1 or 4) rows of inner teeth in the upper jaw and 1 to 3 (usually 2, rarely 4) in the lower.

Lower pharyngeal bone and teeth. Despite some individual variability, the lower pharyngeal bone of *H. obtusidens* is always obviously thickened and the two median rows of teeth are enlarged and molariform or sub-molariform. As might be expected, there is a positive correlation between size and the degree to which the pharyngeal bones and teeth are enlarged. In fishes over 90 mm. S.L. as many as six rows of teeth may be composed of molariform elements; even in specimens with a few molariform rows the remaining teeth are enlarged, except in the upper corners of the bone.

Osteology. In all respects except the form of the pharyngeal apophysis, the neurocranium of *H. obtusidens* resembles that of *H. empodisma*; the pharyngeal apophysis, however, is stouter and broader, thereby foreshadowing the condition found in *H. ishmaeli* and *H. pharyngomylus*. In both these species the basioccipital facets are more expanded than in *H. obtusidens*.

Coloration in life. Sexually active males. Ground colour light blue-black with, ventrally, a silver patch extending from the isthmus almost to the vent ; branchiostegal membrane black. Dorsal fin dark with red lappets and margin to the soft part and red spots or dashes between the branched rays. Caudal dark with a blood-red margin and a diffuse red centre. Anal dark proximally, blood-red distally ; ocelli orange or orange-red. Pelvic fins black. *Quiescent males* as for females but lacking the red spots or flush on the dorsal fin. *Females.* Ground colour silver-grey. Dorsal fin dark with traces of a red flush. Caudal dark. Anal and pelvic fins yellowish.

Preserved material. Adult males. Ground colour brownish, dusky ventrally (below the level of the lower lateral line), with faint indications of four transverse stripes originating from the dark area but not reaching the base of the dorsal fin ; the intensity of the dusky area varies considerably, from charcoal to coal-black. Dorsal fin hyaline to dusky, the basal region and the lappets black ; soft part of the fin sometimes maculate. Caudal dark on its proximal half, light (yellowish) distally. Anal dark on the basal half to third, light distally, with two large white ocelli. Pelvic fins black. *Females* silver-grey to yellowish-brown ; in some fishes there are very faint indications of four to six, incomplete transverse bars on the flanks. Dorsal fin dark or hyaline. Caudal dark, the upper half maculate in some individuals. All other fins hyaline.

Note on four atypical individuals. Four specimens, 80–94 mm. S.L. (B.M. (N.H.) Reg. Nos. 1959.4.28.236–239) from Old Bukakata Bay, Uganda are included in the description given above although they differ from the generality of specimens in certain characters. The lower pharyngeal bones in two of these fishes are somewhat more slender than is modal but are typical in the other two specimens. All four fishes have fewer upper outer teeth than is usual (40–52 cf. modal range 66–70) and somewhat shallower cheek than equivalent sized specimens from other areas. In this latter character, however, they resemble the two type specimens. Finally it must be mentioned that these fishes resemble one another in general facies rather more closely than they resemble the other specimens. Such obvious but undefinable and geographically localized facies are fairly common amongst Lake Victoria *Haplochromis* species.

The exact status of the four specimens from Bukakata cannot be determined for want of more material from this locality.

Distribution. Known only from Lake Victoria.

Ecology. Habitat. Haplochromis obtusidens is predominantly a species of shallow water (less than 30 feet), apparently restricted to a substrate of soft, organic mud ; a few individuals have, however, been taken over sand and in water about 60 feet deep.

Food. The gut contents of forty-six fishes (from numerous localities) indicate that the principal food organisms of *H. obtusidens* are insects (especially larval Diptera) and molluscs (particularly the bivalve *Corbicula*, although some gastropods

[*Melanoides*] are also eaten). Together with these organisms, the fishes had ingested fairly substantial quantities of bottom mud, which, in the areas inhabited by *H. obtusidens*, is almost entirely composed of living and moribund diatoms. A comparison of stomach and intestinal contents shows that the protoplasm of these diatoms is digested by the fish. Other plants, in this case mostly blue-green algae, are apparently undigested.

Breeding. *Haplochromis obtusidens* is a female mouth-brooder ; exact spawning sites were not discovered. A male 83 mm. S.L. is the smallest mature fish in the sample studied ; the smallest mature female is 89 mm. S.L. Both sexes reach the same maximum adult size.

Affinities. The relationships of *H. obtusidens* seem to lie with *H. empodisma* which it resembles in body-form and most syncranial characters. *Haplochromis obtusidens* differs in having an enlarged neurocranial apophysis for the upper pharyngeal bones and in the correlated character, enlarged pharyngeal bones and teeth. The species also shows certain fairly marked affinities with *H. ishmaeli* and *H. pharyngomylus* and could well represent the extant version of an ancestral type from which these two species evolved (see also p. 265).

In Lake Edward, *H. malacophagus* Poll has reached a comparable evolutionary stage leading towards extreme pharyngeal hypertrophy, but the two species are not closely related.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.531	Buganga	Degen
,, 1959.4.28.204–212	Pilkington Bay	E.A.F.R.O.
,, 1959.4.28.213–218	Ekunu Bay	,,
,, 1959.4.28.228–229	Pilkington Bay	,,
,, 1959.4.28.236–239	Old Bukakata Bay	,,
,, 1959.4.28.243–244	Dagusi Island	,,
,, 1959.4.28.245	Buka Bay	,,
,, 1959.4.28.247	Sesse Islands	,,
	Kenya	
,, 1909.7.27.43	Kavirondo Bay	Alluaud
,, 1959.4.28.219–227	Off Port Southby	E.A.F.R.O.
,, 1959.4.28.230–232	Kach Bay (Kavirondo Gulf)	,,
,, 1959.4.28.240–241	Beach below Usoma lighthouse	,,
,, 1959.4.28.242	Off Port Southby	,,
,, 1959.4.28.246	Kavirondo Gulf	,,
,, 1959.4.28.248	Off mouth of Nzoia River	,,
	Tanganyika	
,, 1959.4.28.233–235	Beach near Majita	,,
	Lake Victoria, Locality Unknown	
,, 1928.5.30.21 (Lectotype)	—	M. Graham
B.M. (N.H.).—1928.5.20.20 (Paratype)	—	,,

Haplochromis pharyngomylus Regan 1929

(Text-figs. 19 and 20)

Haplochromis ishmaeli (part) Boulenger, 1906, *Ann. Mag. nat. Hist.* (7), **17**, 446;
Idem, 1915, *Cat. Afr. Fish.*, 3, 293; Regan, 1922, *Proc. zool. Soc. London*, 169.
Haplochromis pharyngomylus Regan, 1929, *Ann. Mag. nat. Hist.* (10) **3**, 388.

Description, based on thirty-eight specimens (including the holotype) 70–126 mm. S.L.

Depth of body 33·8–42·0 (M = 38·5) per cent of standard length, length of head 31·5–36·8 (M = 34·6) per cent. Dorsal head profile straight or somewhat curved (occasionally concave between the eyes), sloping fairly steeply. Preorbital depth 13·8–19·0 (M = 16·8) per cent of head, least interorbital width 23·7–28·5 (M = 26·3), length of snout 27·3–33·3 (M = 30·8), diameter of eye 23·0–31·8 (M = 26·5), depth of cheek 19·7–27·0 (M = 24·1) per cent of head. Caudal peduncle 13·6–18·5 (M = 16·2) per cent of standard length, 1·1–1·6 (modal range 1·3–1·5) times as long as broad.

Mouth horizontal or slightly oblique, jaws equal anteriorly, the lower 35·8–44·0 (M = 38·6) per cent of head, 1·3–2·0 (mode 1·4) times as long as broad. Posterior tip of the maxilla reaching or almost reaching the vertical to the anterior orbital margin.

Gill rakers moderately stout, 6–8 (mode 7), rarely 9, on the lower part of the first arch, the lowermost 1 or 2 rakers reduced.

Scales ctenoid; lateral line with 30 (f.1), 31 (f.6), 32 (f.12), 33 (f.13), 34 (f.4) or 35 (f.1) scales; cheek with 3 or 4 series. Six or 7 (less frequently 8) scales between the lateral line and the dorsal fin, 7 or 8 (less frequently 6 or 9, rarely 10) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.7), 25 (f.28) or 26 (f.3) rays, anal with 11 (f.5), 12 (f.28) or 13 (f.5), comprising XV–XVI, 8–10 (rarely 11) and III, 8–10 spinous and branched rays for the fins respectively. Pectoral 68·5–91·0 (M = 79·6) per cent of head. Caudal truncate.

Teeth. In fishes 70–90 mm. S.L. only unequally bicuspid, relatively stout teeth occur in the outer row of both jaws. Fishes 90–100 mm. S.L. show some variability in the form of these teeth, which may be unicuspids, a mixture of bi- and weakly bicuspid teeth or both bi- and unicuspids. There are 30–42 (mode 36, modal range 36–40) outer teeth in the upper jaw.

Teeth in the inner rows are usually tricuspid in fishes less than 100 mm. S.L. In larger individuals these teeth may be tricuspid or there can be a mixture of tri- and weakly tricuspids; it is uncommon to find only unicuspid teeth in the inner rows. There are 2 or 3 (rarely 4) rows in the upper jaw and 1 or 2 (rarely 3) in the lower.

Lower pharyngeal bone and teeth. With one exception, the lower pharyngeal bone is massive, even in the smallest specimens. Nevertheless, a slight size correlated increase in relative stoutness can be detected in large fishes. Apart from *H. ishmaeli* (p. 277) and *Astatoreochromis alluaudi*, no other Lake Victoria Cichlidae have such large pharyngeal bones.

The exceptional specimen mentioned above was caught near Jinja and measured 98 mm. standard length. The lower pharyngeal of this fish can be compared with that of an *H. obtusidens* of a similar size. Since in all other respects this fish resembles *H. pharyngomylus* more closely than *H. obtusidens* it is included in the description of *H. pharyngomylus*. Four other specimens with even finer pharyngeal bones and dentition, but otherwise resembling *H. pharyngomylus*, are not included in the description but are dealt with in a separate appendix (p. 274).

The lower pharyngeal teeth of *H. pharyngomylus* are large and molariform except for a few teeth situated in the upper, lateral angles of the bone. These teeth, although relatively stout, are cuspidate and small; the number of such teeth decreases markedly in the largest individuals. By analogy with other species having enlarged pharyngeals and for which a greater size range of specimens is available is seems likely that small *H. pharyngomylus* should have less massive bones and fewer molariform teeth, confined to the median tooth series (see Greenwood, 1959).

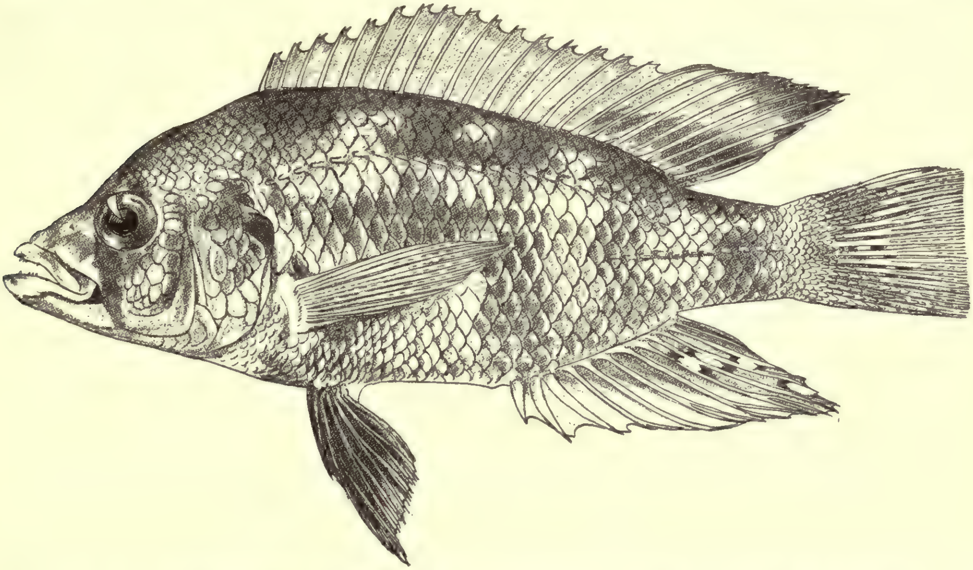

FIG. 19. *Haplochromis pharyngomylus*; holotype. Drawn by Miss M. Fasken.

Osteology of the neurocranium. Apart from an enlarged and strengthened articular apophysis for the upper pharyngeals, the neurocranium of *H. pharyngomylus* is that of a large, generalized *Haplochromis*. The apophysis has been figured and described previously (Greenwood, 1954). Compared with the apophysis of *H. obtusidens* that of *H. pharyngomylus* has a greater surface area and the prootic buttresses are more obvious. These characters are clearly correlated with the more massive pharyngeal bones and musculature of *H. pharyngomylus*. Only slight difrences exist in the apophyseal region of *H. pharyngomylus* and *H. ishmaeli*; but both species differ from *Astatoreochromis alluaudi* in the form taken by the various elements contributing to the apophysis (Greenwood, 1959. In that paper, I also briefly described the possible effects and interactions of genetical and environmental factors on the development of apophyseal form and size in mollusc-crushing species).

Coloration in live fishes. Adult males. Ground colour blue-grey overlying silver; a distinct coppery sheen on the flanks. Dorsal fin hyaline with pinkish lappets and margin to the soft part. Anal hyaline, ocelli yellow. Caudal hyaline with a pink flush most intense distally and on the ventral half of the fin. Pelvics black. *Females.* Golden-green, becoming silvery-white ventrally. Dorsal and anal fins dark; the caudal yellowish-green, darker proximally.

Preserved material. Adult males. Greyish, darker in sexually active individuals; a dark lachrymal stripe sometimes visible; barring on the flanks variable, but usually consisting of seven to ten narrow vertical bars and a very faint longitudinal stripe following the course of the upper lateral line. Dorsal fin hyaline, dark basally in juvenile and quiescent fishes but almost black in sexually active individuals; lappets dark, the soft dorsal intensely maculate in sexually active fishes. Anal hyaline, dark basally, with five or six ocelli arranged in one or two horizontal rows. Caudal hyaline in quiescent fishes, dusky in active ones. Pelvics hyaline in juveniles, black in adults. *Females,* silvery-grey to light brown; striping variable; when present, as described for males. Dorsal fin hyaline or greyish, the soft part weakly maculate in adults. Caudal hyaline or dark, the upper half faintly maculate in some specimens. Anal and pelvic fins hyaline.

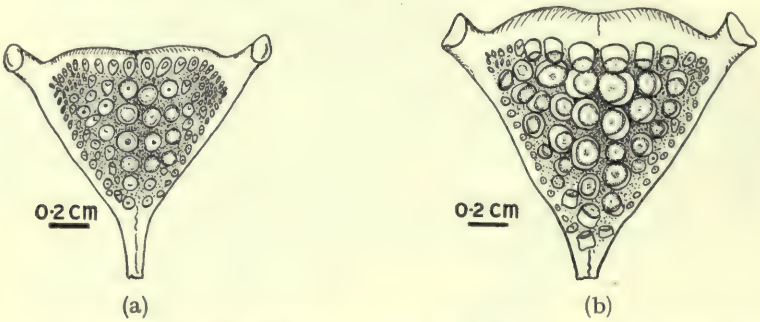

FIG. 20. *Haplochromis pharyngomylus*; lower pharyngeal bone, in occlusal view, of (*a*) a fish 98 mm. S.L., and (*b*) a fish 126 mm. S.L.

Distribution. Known only from Lake Victoria.

Ecology. Habitat. Haplochromis pharyngomylus is apparently confined to water less than 40 feet deep and to areas of the lake where the bottom is hard (sand, shingle or, less frequently, rock); the species is often found amongst stands of aquatic plants. A few specimens have been caught in the areas of intergradation between sand and mud substrates.

Food. Analyses of stomach and intestinal contents from thirty specimens (representing most localities) show that fishes in the size-range 75–115 mm. S.L. feed mainly or even exclusively on Mollusca; only one fish had eaten mollusca and insect larvae. The sample examined also indicated that both bivalves and gastropods are eaten in approximately equal proportions. The fragmented shells do not permit accurate identification of the prey species ; *Sphaerium* sp. and *Corbicula* sp. were recognized amongst the bivalve remains and *Melanoides tuberculata* (the predominant snail), *Bellamya* and less frequently *Biomphalaria* amongst the gastropod fragments.

It is clear from the small size of most shell fragments that the pharyngeal mill in *H. pharyngomylus* is an efficient crushing mechanism. Yet, despite this powerful barrier some shells do pass into the stomach almost undamaged. Since these shells are invariably empty it seems that the digestive enzymes (especially those of the stomach) are capable of breaking down the bodies of snails without preliminary and physical assistance from the pharyngeal teeth. Trewavas (1938) noticed that the gut contents of *H. mahagiensis* (a mollusc eater from Lake Albert) were " impregnated and held in a hard mass by botryoidal aggregates of calcite. Whether these were formed before or after death and fixation is a matter for conjecture." My observations on the gut contents of *H. pharyngomylus* support Trewavas' observations only when the material had been fixed in formol. This would suggest that the calcite aggregates are formed as a result of a chemical reaction between the slightly acid formol and the calcium of the shell. I have never observed aggregates in fresh gut contents, where the various shell fragments could be separated easily.

Breeding. The actual spawning sites and breeding behaviour of *H. pharyngomylus* are unknown, but females carrying embryos and larvae in the buccal cavity occur together with non-breeding fishes in most localities. The smallest adult recorded is a female 90 mm. S.L. ; the smallest adult male is 94 mm. S.L. Both sexes reach the same maximum adult size.

Affinities and diagnosis. Extreme hypertrophy of the pharyngeal mill serves to set *H. pharyngomylus* apart from all except one species of Lake Victoria *Haplochromis*. The other species is *H. ishmaeli* which appears to be very closely allied to *H. pharyngomylus*. Although in structural characters the two species are similar an experienced observer can, in most instances, readily distinguish between the two species. But, as is so often the case with *Haplochromis*, the subjective characters used for " field " identifications cannot be quantified or adequately described on paper. When seen alive, adult males of the two species have distinctive coloration.

Haplochromis pharyngomylus is distinguished from *H. ishmaeli* by the following characters : fewer outer teeth in the upper jaw (30–42, modal range 36–40 cf. 38–66, modal range 44–52 in *H. ishmaeli*); shorter pectoral fin (68·0–91·0, M = 79·6 per cent of head cf. 75·0–102·0, M = 88·5) ; differences in male breeding coloration (see p. 272 and p. 277) and differences in habitat preference (*H. pharyngomylus* is essentially a species of hard substrates whilst *H. ishmaeli* shows a marked preference for muddy areas). With the exception of differences in male breeding colours, none of these characters alone is trenchant ; taken together, however, they provide fairly reliable diagnostic features.

The phylogenetic position of *H. pharyngomylus* has been discussed above (p. 269) and in an earlier paper (Greenwood, 1954).

In Lake Edward, *H. placodus* Poll represents the equivalent evolutionary phase in the development of hypertrophied pharyngeals. *Haplochromis placodus* and *H. pharyngomylus* could be derived from a common ancestral stem, but of course, the two species could equally well be examples of convergent evolution.

APPENDIX

Four specimens (115–120 mm. S.L.) from Jinja (B.M. (N.H.) Reg. No. 1959.4.28.352–355) bear a strong resemblance to *H. pharyngomylus* except that the lower pharyngeal bone in these specimens is barely enlarged and the pharyngeal dentition is correspondingly weak. These fishes cannot be distinguished from *H. pharyngomylus* on proportional measurements, teeth of jaws, fin and scale counts, general appearance or preserved coloration. All four fishes are adult males but unfortunately their live coloration was not recorded.

From *H. pharyngomylus* material described above and from field observations on numerous other specimens it is clear that intraspecific variability in the enlargement of the pharyngeal bones is slight and mainly correlated with size. No specimens were found which could be considered intermediate between the typical condition for the species and that seen in the aberrant individuals. On the other hand, a study of *Astatoreochromis alluaudi* (a *Haplochromis*-like monotypic genus) showed that some populations have enlarged pharyngeals whilst others exhibit only slight hypertrophy of these bones (Greenwood, 1959).

Thus for the moment it is impossible to dismiss the possibility that the four "*pharyngomylus*"-like fishes are indeed aberrant members of that species. I do not propose, however, to include them in this revised description or to describe them as distinct species until further collections dictate one step or the other.

Study material and distribution records

Museum and Reg. No.		Locality	Collector
		Uganda	
B.M. (N.H.).—	1906.5.30.383	Entebbe	Degen
,,	1907.5.7.71	Buddu Coast	Simon
,,	1958.12.5.30–33	Entebbe	Pitman
,,	1959.4.28.317–321	Beach near Nasu Point	E.A.F.R.O.
,,	1959.4.28.322–326	Entebbe, Harbour	,,
,,	1959.4.28.327–329	Entebbe, Airport beach	,,
,,	1959.4.28.333–334	Beach near Grant Bay	,,
,,	1959.4.28.335–336	Between Yempita and Busiri Isls., Buvuma Channel	E.A.F.R.O.
,,	1959.4.28.340–343	Beach near Hannington Bay	,,
,,	1959.4.28.344	Entebbe, Harbour	,,
,,	1959.4.28.345–347	Napoleon Gulf, near Jinja	,,
,,	1959.4.28.351	Ramafuta Island	,,
,,	1959.4.28.358	Jinja Pier	,,
		Kenya	
,,	1959.4.28.348	Kasingiri Gingo (Kavirondo Gulf)	,,

Study material and distribution records (*cont.*)

Museum and Reg. No.		Locality	Collector
		Tanganyika	
,,	1959.4.28.337–339	Majita	,,
,,	1959.4.28.349	Beach near Majita	,,
,,	1959.4.28.350	Mwanza, Capri Bay	,,
		Lake Victoria, Locality Unknown	
,,	1928.5.24.313 (Holotype)	—	M. Graham
,,	1959.4.28.330–332	—	E.A.F.R.O.

Haplochromis ishmaeli Blgr. 1906
(Text-fig. 21)

Haplochromis ishmaeli (part) Boulenger, 1906, *Ann. Mag. nat. Hist.* (7), **17**, 446; *Idem*, 1915, *Cat. Afr. Fish.* **3**, 293; Regan, 1922, *Proc. zool. Soc. London*, 169.
Tilapia pallida (part) Boulenger, 1911, *Ann. Mus. Genova* (3), **5**, 74; *Idem*, 1915, *tom. cit.*, 231–2.
Labrochromis pallidus Regan, 1920, *Ann. Mag. nat. Hist.* (9), **5**, 45 (footnote).
Tilapia martini (Part) Boulenger, 1915, *tom. cit.*, 239.
Paratilapia victoriana (part) Boulenger, 1915, *tom. cit.*, 341.
Haplochromis macrops (part) Regan, 1922, *Proc. zool. Soc. London*, 166.

In the original description of *H. ishmaeli*, Boulenger listed thirteen type specimens (syntypes) all collected by Degen at Bunjako, Uganda. However, only eleven specimens (ten in spirit and one skeleton) answering this description can be found in the collections of the B.M. (N.H.); furthermore, only eleven such specimens are recorded in the Museum's catalogue of accessions. That the number thirteen was a slip of the pen seems certain because Boulenger (1915) only lists ten types from Bunjako in the third volume of his Catalogue of Fresh-water Fishes of Africa. The only other specimen from this locality is listed in the " Catalogue " as a skeleton and is presumably the eleventh syntype.

These figures agree with the number of specimens I could locate and, more important, they agree with the number registered in the Museum's record of accessions. But, the situation is still somewhat obscure because in the " Catalogue " (*tom. cit. loc. cit.*) Boulenger lists as a type a specimen collected from *Entebbe*; since no reference is made to this fish in the original description I am treating its later inclusion in the list of types as erroneous.

Note on the genus Labrochromis, Regan, 1920. This genus, briefly described in a footnote to Regan's paper on the genera of Tanganyika cichlids was apparently based on a single specimen prepared from one of the syntypes of *T. pallida* (B.M. (N.H.) Reg. No. 1911.3.3.132). In his revision of the Lake Victoria Cichlidae, Regan (1922) correctly identified this skeleton as being that of *Haplochromis ishmaeli* and abandoned the genus *Labrochromis* on the grounds that, apart from possessing hypertrophied pharyngeals, *H. ishmaeli* is " nearly identical with *H. cinereus*." Whilst I do not agree with the latter part of this statement, I fully endorse Regan's action in not maintaining the monotypic genus *Labrochromis* for *Haplochromis ishmaeli*.

Lectotype of Haplochromis ishmaeli. An adult female 104·0 + 23·0 mm. total length (B.M. (N.H.) Reg. No. 1906.5.30.400) collected by Degen at Bunjako, Uganda.

Description, based on thirty-five specimens (including the lectotype and two paratypes) 82–136 mm. S.L., all from Lake Victoria. Two specimens from Lake Edward are described separately on p. 278.

Depth of body 37·0–45·5 (M = 40·1) per cent of standard length, length of head 33·8–37·5 (M = 34·8) per cent. Dorsal head profile slightly curved or straight, sloping fairly steeply. Preorbital depth 15·3–20·5 (M = 17·0) per cent of head, least interorbital width 24·0–32·0 (M = 27·6), length of snout 29·0–36·0 (M = 31·6), diameter of eye 23·0–31·0 (M = 27·7), depth of cheek 20·7–31·0 (M = 25·5) per cent. Caudal peduncle 14·6–18·8 (M = 17·6) per cent of standard length, 1·2–1·6 (modal range 1·3–1·5) times as long as deep. Jaws equal anteriorly, the lower 35·8–42·5 (M = 39·1) per cent of head and 1·4–2·0 (modal range 1·4–1·6) times as long as broad. Mouth horizontal or very slightly oblique; the posterior tip of the maxilla reaching the vertical through the anterior orbital margin or somewhat beyond, rarely not quite reaching the orbit.

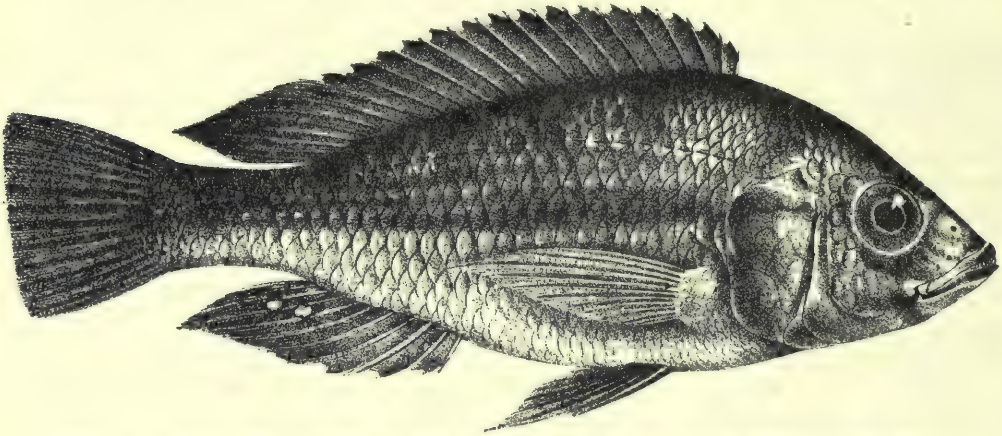

FIG. 21. *Haplochromis ishmaeli:* lectotype (from Boulenger, *Fishes of the Nile*).

Gill rakers stout, but relatively slender in a few specimens; 6–8 (mode 7), rarely 9, on the lower part of the first arch, the lowermost one or two rakers usually reduced.

Scales ctenoid; lateral line with 30 (f.3), 31 (f.8), 32 (f.15), 33 (f.5) or 34 (f.4) scales; cheek with 3 or 4 rows. Five to 7 (rarely 8) scales between the lateral line and the dorsal fin origin; 8–9 (occasionally 7) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.1), 24 (f.13) or 25 (f.21) rays, anal with 11 (f.13), 12 (f.21) or 13 (f.1) comprising XV–XVI, 8–10 and III, 8–10 spinous and branched rays for the fins respectively. Pectoral fin 75·0–102·0 (M = 88·5) per cent of head. Caudal truncate or subtruncate.

Teeth. The outer row in both jaws usually contains a mixture of relatively stout, unequally bicuspid and unicuspid teeth; less frequently only unicuspids occur in this row. There is apparently no size-correlated difference in the type or the number of teeth present. There are 38–66 (modal range 44–52) teeth in the outer row of the upper jaw.

Teeth in the inner series are generally tricuspid, but in some fishes the entire inner series are composed of unicuspids. There are 2 or 3 (rarely 1) rows of teeth in the upper jaw and 1 or 2 (less commonly 3) rows in the lower. The inner teeth are implanted somewhat obliquely.

Lower pharyngeal bone and teeth. The lower pharyngeal bone in *H. ishmaeli* is massive and almost all the teeth are molariform ; only those situated in the posterior angles of the bone remain small, with pointed crowns. There is some individual variation in the relative enlargement of the bone, but this is slight in comparison with the variation known from such species as *H. obtusidens* and *Astatoreochromis alluaudi*. A slight size-correlated increase in the relative stoutness of the pharyngeal bones was observed in the material studied ; likewise, there is an increase in the number of molariform teeth in larger fishes.

In size, shape and dentition, the pharyngeal bones of *H. ishmaeli* are directly comparable with those of *H. pharyngomylus*.

Neurocranial osteology. The neurocranium of *H. ishmaeli* is virtually identical with that of *H. pharyngomylus*.

Coloration of live fishes. Sexually active males. Ground colour light yellow-green dorsally, shading to yellow on the flanks and greyish-white ventrally. Dorsal fin yellow-green, lappets of the anterior spines dusky, the remainder scarlet, as are the spots and dashes between the branched rays. Caudal fin greyish, with red maculae (sometimes coalesced) between the rays. Anal smoky grey with black lappets and an overall scarlet flush ; ocelli yellow. Pelvic fins black. *Females* golden-green shading to silvery-white ventrally, the pectoral region faintly blackish. Dorsal fin hyaline, with a narrow red margin. Anal light yellowish-green. Caudal and pelvic fins pale yellow.

Preserved material. Adult males, yellowish-grey, dusky on the chest and branchiostegal membrane (lighter in sexually quiescent fishes) ; very faint indications of six or seven vertical stripes on the flanks. (These bars are more widely spaced than in *H. pharyngomylus*, see p. 272). A distinct lachrymal stripe. Dorsal fin hyaline in juvenile fishes but darker and with the soft part maculate in mature males ; lappets dark. Caudal hyaline, the upper part often maculate. Anal hyaline, the basal third dark in sexually active individuals ; three to five large, dead-white ocelli arranged in one or, rarely, two rows. *Females*, brownish to yellowish-silver ; sometimes, very faint traces of five to seven transverse bars on the flanks ; a weak lachrymal stripe visible in some fishes. All fins hyaline, the dorsal darkest.

Distribution. Lakes Victoria and Edward.

Ecology. The data given in this section relate to fishes from Lake Victoria ; nothing is known for fishes from Lake Edward.

Habitat. Haplochromis ishmaeli is essentially a species of inshore regions where the water is less than 30 feet deep and the bottom composed of soft, organic mud.

No specimens have been recorded from depths greater than 60 feet, but some have been caught in nets set over sand and shingle substrates. *Haplochromis ishmaeli* would seem to be the ecological (soft substrate) counterpart of *H. pharyngomylus* (solid substrates).

Because of the difficulty in distinguishing *H. ishmaeli* from *H. pharyngomylus* and especially because the latter species was not recognized until after Graham's collections were brought to England, it is impossible to use Graham's (1929) catch records as an additional source of information on the intralacustrine distribution of *H. ishmaeli*.

Food. The stomach and intestinal contents of nineteen fishes (from several localities) indicate that *H. ishmaeli* in the size-range 84–135 mm. S.L. feed almost exclusively on Mollusca ; the few insect larvae found together with snails in the stomach of one fish suggest that insects may be ingested accidentally.

The number of fishes with food remains is insufficient to determine whether bivalves or gastropods predominate in the diet. Slightly more gastropods (*Melanoides tuberculata*) than bivalves (*Corbicula* sp.) were found in the sample examined.

Breeding. No information is available on the breeding sites or habits of *H. ishmaeli* although the number of females with " spent " ovaries and ventrally distended mouths suggests that the species is probably a female mouth-brooder. The smallest mature females are 97 mm. S.L. (but see Appendix 2) and the smallest adult male is 98 mm. S.L. Females apparently reach a greater maximum size than do males.

Affinities and diagnosis of *H. ishmaeli* are discussed on page 273, with reference to its closest relative, *H. pharyngomylus*.

APPENDIX

(1) *Haplochromis ishmaeli* from Lake Edward. I have been able to examine only two specimens from Lake Edward, one an adult female 120·0 + 28·0 mm. long and the other an adult male 118·0 + 27·0 mm. long (see Trewavas, 1933). In general appearance, in most morphometric characters and in scale and fin ray counts the two fishes are indistinguishable from specimens of a similar size from Lake Victoria. The nature of the pharyngeal bones and dentition is also identical. Nevertheless, the Lake Edward fishes do differ slightly in three characters.

(i) The interorbital is somewhat narrower (24·1 and 25·0 per cent of head) than the mean interorbital width of Victoria fishes (27·6 per cent) although still within the range known from this population. (ii) The number of outer teeth in the upper jaw (40 and 42) is in the lower section of the range for Lake Victoria fishes. (iii) The caudal peduncle is stouter in the majority of Victoria specimens. Now that more specimens are available from Lake Victoria, Trewavas' (op. cit.) observation on the larger eye of the Edward specimens is no longer applicable.

None of the differences commented upon above is so marked as those characterizing the Lake Victoria and Lake Edward populations of *Astatoreochromis alluaudi* (Greenwood, 1959).

Nothing is known about the bionomics of *H. ishmaeli* in Lake Edward ; the two specimens studied were caught in a seine net fished from the eastern shore of the lake near Kisenyi.

(2) Three *H. ishmaeli*-like fishes from Lake Victoria. Three specimens (82, 96 and 100 mm. S.L. (B.M. (N.H.) Reg. Nos. 1959.4.28.304–306)) caught in a trawl off the mouth of the Nzoia river, Kenya, present something of a problem. In appearance and in all standard counts and measurements these fishes are typically *H. ishmaeli*. However, their collector, Mr. S. H. Deathe, recorded the live coloration of these fishes as bright pink. Because all three specimens are adult males, I consider that this striking departure from the usual male coloration of *H. ishmaeli* may be significant, especially since pink is not one of the basic colours in *H. ishmaeli* pigmentation. A further interesting difference is that the smallest specimen is sexually mature whereas the smallest adult *H. ishmaeli* recorded is 98 mm. S.L.

Unfortunately I have only these three specimens and I did not see them when alive. Thus, it is difficult for me to assess fully this seemingly outstanding difference in coloration.

No typical *H. ishmaeli* were reported in the same haul and I do not consider that there is enough evidence to decide whether these peculiar individuals represent an aberrant population of *H. ishmaeli* or a distinct species differing from *H. ishmaeli* in the coloration of its adult males.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.400 (Lectotype)	Bunjako	Degen
,, 1906.5.30.401–402*a* (Paratypes)	,,	,,
,, 1906.5.30.396 (Paratype)	,,	,,
,, 1911.3.3.131 (Paratype *Tilapia pallida*)	Jinja	Bayon
,, 1909.5.4.8–10	Sesse Isls.	,,
,, 1906.5.30.275–279	Bunjako	Degen
,, 1959.4.28.281–290	Pilkington Bay	E.A.F.R.O.
,, 1959.4.28.296–300	Ekunu Bay	,,
,, 1959.4.28.301–303	Pilkington Bay	,,
,, 1959.4.28.307–309	Buka Bay	,,
,, 1959.4.28.312–313	Entebbe, Harbour	,,
,, 1959.4.28.314	Macdonald Bay	,,
,, 1959.4.28.316	0° 4′ S., 33° 14′ E.	,,
	Kenya	
,, 1909.11.15.40	Kisumu	A. B. Percival
,, 1959.4.28.274–280	South of Port Southby	E.A.F.R.O.
,, 1959.4.28.356	Kavirondo Gulf	M. Graham
	Tanganyika	
,, 1959.4.28.291–295	Majita	E.A.F.R.O.
,, 1959.4.28.310–311	Beach near Majita	,,

SUMMARY

1. Eleven species are redescribed on the basis of new material.

2. In addition, three new species (*Haplochromis theliodon*; *H. empodisma* and *H. saxicola*) are described.

3. Several phyletic lines are represented amongst these fourteen species, which include *H. cinereus*, a species once thought to represent one of the basic types from which the present-day species-flock had evolved. Evidence now available suggests that, anatomically, *H. cinereus* is not sufficiently generalized to retain this distinction.

4. Notes are given on the feeding habits and bionomics of the species.

5. Three species (*H. obtusidens, H. pharyngomylus* and *H. ishmaeli*) are largely or entirely mollusc-eaters; three others (*H. humilior, H. theliodon* and *H. riponianus*) feed on both insects and molluscs; one, *H. martini*, is a piscivorous predator and seven others are insectivore/omnivores.

6. One species, *H. niloticus* (nom. nov. for *Tilapia bayoni* Blgr. 1911) is known only from the Victoria Nile, whilst *H. ishmaeli* occurs in both Lakes Victoria and Edward; *H. humilior* is found in Lake Victoria and the Victoria Nile.

7. The assumed distribution of *H. macrops* in both Lakes Victoria and Edward is discussed; no definite conclusion can be drawn from the material now available.

8. Two groups of specimens are dealt with in separate appendices because of their uncertain taxonomic position. One group is apparently allied to or even conspecific with *H. pharyngomylus* and the other with *H. ishmaeli*. No conclusion can be reached on the status of these aberrant fishes.

ACKNOWLEDGMENTS

It is with great pleasure that I acknowledge my thanks to Dr. Ethelwynn Trewavas for her advice and criticism and for reading the manuscript of this paper. My thanks are also due to Mr. C. C. Cridland of E.A.F.R.O. Jinja, Uganda, for identifying many of the Mollusca recovered from gut contents.

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Pp. 283–324.
With 1 *Table, Plates* 3–4 *and* 34 *Text-figures.*

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ON A *STYGIOMYSIS* FROM THE WEST INDIES, WITH A NOTE ON *SPELAEOGRIPHUS* (CRUSTACEA, PERACARIDA)

By ISABELLA GORDON, D.Sc., Ph.D.

SYNOPSIS

Stygiomysis holthuisi (Gordon), the second known species of the aberrant Mysidacean genus *Stygiomysis*, is described and figured in detail. The systematic position of the family Stygiomysidae is discussed. It is most closely allied to the family Lepidopidae and both families possess certain characters of the suborder Mysida, others of the suborder Lophogastrida. The paragnatha of some other Mysidacea are figured for comparison with those of *Stygiomysis*. The terminology of the thoracic limbs, and of the segments of the thoracic endopodite, is briefly discussed. A note on *Spelaeogriphus lepidops* Gordon is added, together with a few comments on the systematic position of the order Spelaeogriphacea.

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I. ON *STYGIOMYSIS HOLTHUISI* (GORDON) FROM THE WEST INDIES.

INTRODUCTION.

Dr. L. B. Holthuis of the Rijksmuseum van Natuurlijke Historie, Leiden, kindly sent me for study three specimens of an interesting cavernicolous " shrimp " which he collected in February, 1957 on the island of St. Martin, Lesser Antilles. When I first examined these specimens I thought that, in spite of the long vermiform body and very short carapace, they looked remarkably like Mysidacea. Then, when I discovered some of their most striking peculiarities, I decided that they did not belong to the Order Mysidacea as at present defined. I fully intended to look up all the literature relating to cavernicolous Mysidacea and, had I done so, I certainly would not have referred these specimens to a new genus. But, when I wrote the preliminary note to *Nature* (Gordon, 1958), I did not realise that I had inadvertently omitted to refer to Caroli's 1937 paper on the genus *Stygiomysis*. I have to thank Dr. H. Nouvel of Toulouse for calling my attention to this lapse and I fully agree with him that my genus *Rhopalonurus* is a synonym of *Stygiomysis* Caroli.

The discovery of a second species of *Stygiomysis* so far from the locality of the type species of the genus, which is in Italy, is very interesting. Perhaps this rare genus is, or was at some remote period, widely distributed. Caroli had only four specimens of *Stygiomysis hydruntina* when he published his " nota preliminaire " in 1937. As far as I know, he has never published a fuller description of the species, nor has it been collected again although the two Italian grottos must in all probability have been visited since 1937. I made a fairly complete study of the three type specimens of *Stygiomysis holthuisi* and had finished the description and figures before I read Caroli's *Stygiomysis* paper. By that time I also had come to the conclusion that the species was in fact an aberrant member of the Mysidacea, thus confirming Caroli's opinion. So far no ovigerous female of either species has been found, although in each case a somewhat immature female with only four pairs of developing oostegites is known. Caroli thought it most probable that in *Stygiomysis* the full complement of oostegites will be seven pairs ; within the order Mysidacea there are as a rule either seven pairs of oostegites, or else two or three pairs—*Thalassomysis* established in 1939 has four pairs, the first two of which are small, the last two pairs forming most of the brood pouch. But, as Caroli rightly points out, in no Mysid are oostegites absent from the *last* pair of thoracic limbs. If *Stygiomysis* should prove to have only four pairs, then they would be absent from the last pair of thoracic appendages and quite exceptional.

Recently Dr. Holthuis sent me another specimen from the type locality ; this proved to be a male and the second pair of pleopods differs appreciably from that of the female. Caroli says that in *Stygiomysis hydruntina* none of the pleopods " mostra particolari modificazione sessuali ". This admittedly rather slight sexual dimorphism of the second pair of pleopods is similar to that found in all three monotypic genera of the cavernicolous family Lepidopidae (previously Lepidophthalmidae), to which the family Stygiomysidae appears to be most nearly related.

After the manuscript was finished, I received from the Amsterdam Museum a fifth specimen which Dr. J. H. Stock obtained in the same place on St. Martin on 4th February, 1959.

Order MYSIDACEA

Genus ***STYGIOMYSIS*** Caroli 1937

Stygiomysis Caroli, 1937, p. 220.
Rhopalonurus Gordon, 1958, p. 1552.

DIAGNOSIS. Aberrant cavernicolous Mysidacea with body rather vermiform, somewhat depressed. Carapace short, smooth, fused with tergites of first four thoracic somites, not produced antero-laterally beyond the minute rostral apex and lacking the usual postero-lateral " wings " so that thoracic somites 5 to 8 are *entirely exposed*. Division of the long thorax into subtagmata further emphasized by the modification of the first *four* pairs of thoracic limbs to assist in feeding (maxilliped and gnathopods—see p. 315), the last four pairs being slender peraeopods. Abdomen widest across third somite, sixth somite *shorter* than fifth. Telson almost as wide as long; spines on truncate posterior margin only. Ocular scales broader than long, without trace of pigment or visual elements. Antennula more robust and rather longer than antenna, the inner flagellum slightly longer than carapace. Antennal scale minute; both segments of antennal protopodite distinct (peduncle therefore four-segmented). Labrum broadly triangular. Labium with long, pendant, widely separated paragnatha which conceal part of mandibles. Mandibles with well developed incisior, poorly developed molar, process and a distinct spine-row; a number of long simple spines on minute third segment of the palp. Maxillula without reflexed palp, distal endite unusually large and robust, the anterior apical spine very large. Maxilla beset with strong spines rather than setae; the two segments of endopodite very short. Maxilliped (first thoracic limb) pediform, without endites or lobes; exopodite a small unsegmented lamella; epipodite rather short and broad. Thoracic appendages 2 to 8 each with well developed multiarticulate exopodite; endopodites 2 to 4 modified as gnathopods, forwardly directed and stronger than those of the peraeopods (5 to 8). Penultimate segment of thoracic endopodites not subdivided. Pleopods all reduced, biramous, with one-segmented endopodite and three-segmented exopodite (exopodite two-segmented in male pleopod 2); alike in both sexes, apart from the sexual dimorphism exhibited by pleopods 2 in *Stygiomysis holthuisi*. A transverse chitinous lamella, or pair of lamellae, with which the protopodites of the pleopods are incorporated, projects from the posterior sternal margin of abdominal somites 3 to 5. Uropods unusual in having a long, stout, backward prolongation of the protopodite, armed with strong curved spines; statocyst absent. Oostegites at least four pairs, but the full complement is unknown (Caroli thinks it may be seven pairs).

Type species: *Stygiomysis hydruntina* Caroli 1937, from Italy. A second species from the West Indies is described below.

Stygiomysis holthuisi (Gordon)

Rhopalonurus holthuisi Gordon, 1958, p. 1552.

MATERIAL. The holotype, a female with developing oostegites measuring 9 mm. in length; the larger paratype is a slightly immature female without oostegites, the smaller paratype is probably immature.[1] In addition to the three original specimens, I received from the same locality at a later date, a male measuring 10 mm. in body length (also in the Leiden Museum).

LOCALITY. Devil's Hole, near Simson's Bay (or Simpson's Bay), in the Dutch part of St. Martin, Lesser Antilles, 10th February, 1957, (the three types) and, 25th May, 1958 (one male).

---

[1] The holotype and smaller paratype are in the Leiden Museum Collection, and are registered as Crust. G. 434 and Crust. G. 435 respectively. The larger paratype is in the British Museum (reg. no. 1959.vii.3.1).

HABITAT. " Devil's Hole lies to the south east of Simson's Bay bridge near the southern shore of St. Martin, just east of Simson's Bay. It is a sink-hole about 5 m. deep in a limestone slope. The hole itself is wide and rather easily accessible. From the hole a few short dead-ending passages run inwards. In one of these passages, which is about 10 m. long, there is a small puddle, about 30 cm. in diameter and 10 to 20 cm. deep. A film of limestone particles covered the larger part of the surface, and a limestone sediment on the bottom made the water turbid when stirred. The water tasted saltish, its salinity being 8100 mg. Cl/litre. It was not in total darkness as the entrance of the passage could still be seen. The distance of the sink-hole from the sea is about 300 m."

Dr. Holthuis returned to the same pool two days later, but did not obtain any specimens of *Stygiomysis holthuisi*, although he got a few Amphipods which he had not seen during his first visit to the cave. Dr. P. Wagenaar Hummelinck, who collected in the same locality on 26th July, 1955, obtained only Amphipods and Nematodes. (Information supplied by Dr. L. B. Holthuis.)

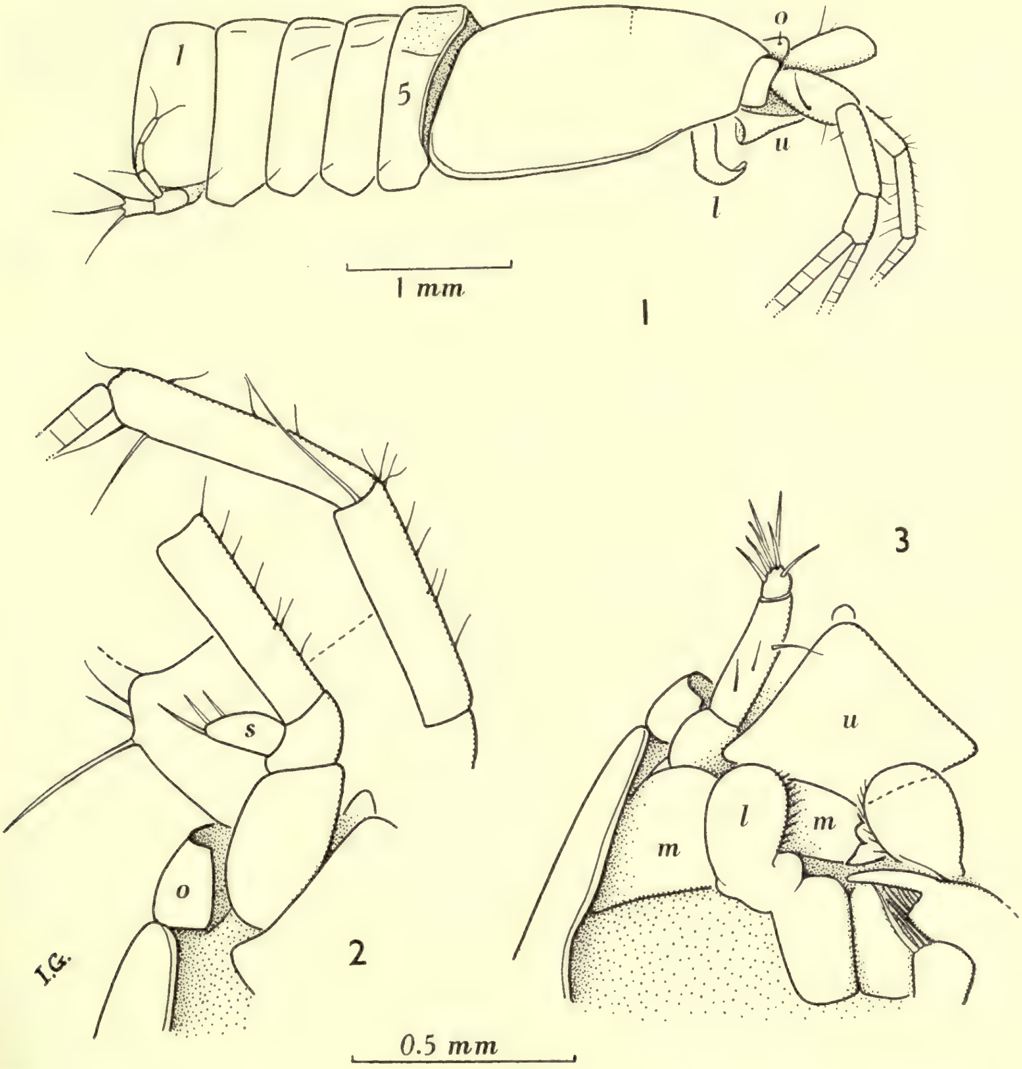
ADDITIONAL MATERIAL. A fifth specimen was received after the manuscript was finished. It was found in a small hole or pitch a few inches square, in the type locality, Devil's Hole, St. Martin, by Dr. J. H. Stock on 4th February, 1959. It is a slightly immature specimen, probably female, without oostegites, and is in the Amsterdam Museum.

DESCRIPTION OF FEMALE.

The largest specimen, measuring 9 mm. in length, and selected as the holotype, is represented in Plate 3. The long, narrow, rather vermiform body is flattened dorsoventrally and is fully segmented behind the carapace, which is just over one-fourth of the total length. The ratio of length to maximum width of *carapace* is 1·6 : 1 and the surface is smooth (with perhaps the merest hint of the cervical furrow). The carapace is completely fused dorsally with the tergites of thoracic somites 1 to 4, being free only at the sides to enclose long narrow branchial chambers. The anterior margin, on either side of the median triangular apex, which scarcely merits the name of rostrum is rather oblique and slightly concave. In front of each concavity is a short broad scale, presumably an ocular scale without any trace of pigment or visual elements, ((Pl. 3 and Text-figs. 1–3, *o*). This scale curves downwards and inwards as shown in Text-figs. 2 and 3. The posterior margin of the carapace does not overlap any part of the fifth (first free) thoracic somite ; indeed it is slightly overlapped by the latter in the mid-dorsal line (Text-fig. 1 and Pl. 3, *5*).

The four free thoracic somites pass imperceptibly into the *abdomen*, although the two tagmata can easily be recognized by their respective appendages. Together they form a very elongated barrel (in dorsal aspect), widest across abdominal somites 2 and 3 ; abdominal somites 4 and 5 are longest and equal. The *telson* is as long as the fifth and sixth abdominal somites together, and is nearly as broad as long. The lateral margins are only slightly convergent and the wide posterior margin is armed with strong spines namely, three at each side and a median one flanked by a pair of shorter spines ; four or five spinules fill the gaps between lateral and median spine groups (Pl. 3 ; only the median group is visible in Text-fig. 8).

The *antennula* is longer, and much stouter, than the antenna and is biramous (Text-fig. 1 and Pl. 3). Of the three segments in the protopodite the second is the longest, the first or basal one the widest. The flagella are only slightly unequal in length, the inner one is the more slender, with about 28 segments whereas the outer



FIGS. 1–3. *Stygiomysis holthuisi* (Gordon). Fig. 1. Larger paratype, anterior half of body in lateral aspect, after removal of the mouthparts and some thoracic appendages. Fig. 2. Antero-lateral angle of carapace, basal segment of antennula and antennal peduncle, part of labrum. Fig. 3. Right anterior portion of body, in ventral aspect.

l. Paragnath of lower lip. *m*. Mandible. *o*. Ocular scale. *s*. Antennal scale. *u*. Upper lip or labrum. 5. Fifth (first free) thoracic somite. 1. First abdominal somite.

one has only 16 to 18 longer segments most of them with long sensory hairs or aesthetascs on the inner margin. The antennulae arise beneath the ocular scales and are not widely separated.

The *antenna* is shorter and much more slender than the antennula. The peduncle of the right antenna of the larger paratype is represented, highly magnified, in Text-fig. 2. The protopodite seems to have only two segments; the basal one is nearly twice as long as wide, the second one is short and bears, at its outer distal angle, a minute exopodite or scale (s). The two basal segments of the endopodite are each long and slender (at least four times as long as wide) and the flagellum, which has 16 to 18 segments, is about four-fifths of the carapace length (Pl. 3).

Mouthparts. Those on the right side of the larger paratype were removed for detailed examination. Each appendage was sketched from various aspects before any attempt was made to stain and mount it. In this way any distortion due to movement of, or pressure from, the coverslip was eliminated. Certain details not apparent in the unstained appendages were inserted later from the micro-preparations.

The *labrum* or upper lip is large and triangular, with rounded apex, beyond which, at a lower level, a small rounded lobule is visible (i.e. the lobule is more dorsal in position)—see Text-figs. 1 and 3, *u*. Behind the mandible is the *labium* or lower lip which is unusual in that the paragnatha are widely separated; moreover, each is enormous, pendant and forwardly directed so as to overlap and partially conceal the mandible (Text-figs. 1 and 3, *l*). The right mandible is shown *in situ* in Text-fig. 3 and the distal portion is represented in Text-fig. 4. The crown consists of a well developed, three-lobed incisor process (with a subsidiary tooth at the base of one of the lateral ones) a small but well chitinized knob-like molar process and, between the two processes, a strongly chitinized triangular lobe† and a row of five graded spines. The palp has the usual three segments; the median one is very long and somewhat twisted, the short terminal one has seven long spines. The *maxillula* is unusually large and massive (Text-fig. 5). The proximal endite, Hansen's lobe 1, has four terminal spines, two long and plumose, two short and simple. The distal or major endite, Hansen's lobe 3, has a terminal row of spines the anterior one unusually long and stout and, near its base, is a long seta. There is no backwardly directed endopodite or palp. The *maxilla* is a thin leaf-like appendage abundantly beset with spines and setae (Text-fig. 6). Hansen's pl. 3 was not apparent until the appendage had been stained and mounted. The proximal endite (*s*), in this case the lobe from 2, is simple, with a median seta on the posterior margin and a series of apical and subapical spines. The endite from pl. 3 (*d*) is divided into a small distal lobe with four terminal spines, and a large oval proximal lobe with a row of nine marginal spines. A short, two-segmented endopodite (*en*) follows; the distal segment bears three long spines, the proximal one has two spines on the inner margin. A long narrow exopodite (*ex*) arises from the outer margin of pl. 3; its margins, the free inner one excepted, bear plumose setae.

The *first thoracic appendage* or maxilliped is represented in Text-fig. 7 at a lower magnification than the other mouth parts. Though much smaller than, it is essenti-

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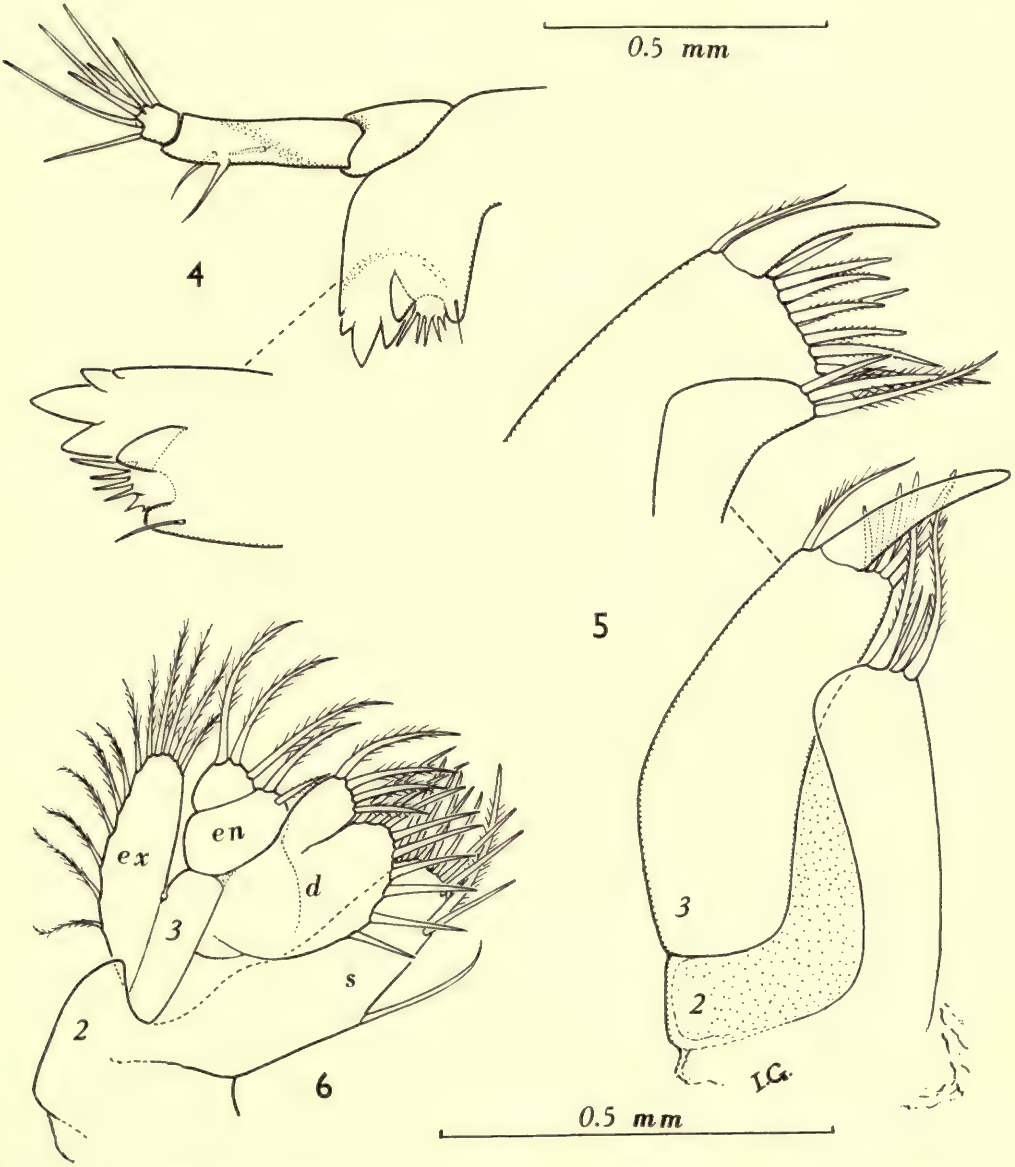
† The fixed lacinia, against which the *lacinia mobilis* works.

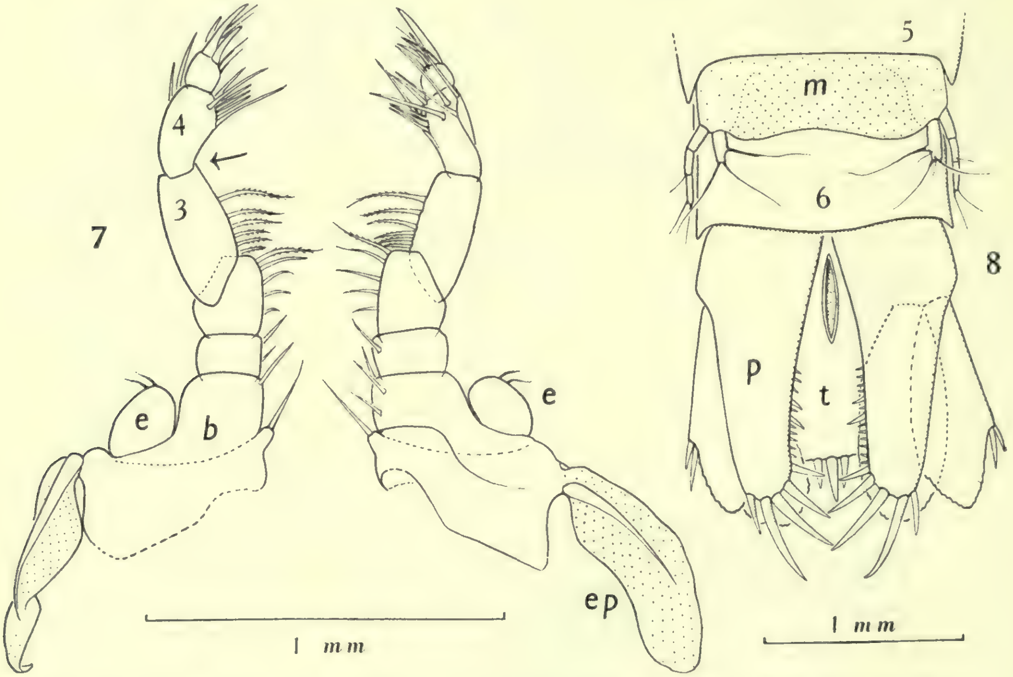
ally similar to, the three following pairs of thoracic limbs. However, it alone bears a fairly large epipodite reflexed into the brancial chamber and, moreover, the exopodite is reduced to a small oval unsegmented lamella (which may also be respiratory).



FIGS. 4–6. *Stygiomysis holthuisi* (Gordon). Mouthparts of larger paratype. Fig. 4. Distal portion of right mandible, with palp. Fig. 5. Right maxillula. Fig. 6. Right maxilla. All at higher scale except upper Fig. 4.

d. Divided endite. *en.* Endopodite. *ex.* Exopodite. *s.* Simple or undivided endite. 2 and 3 Hansen's plates 2 and 3 of protopodite (coxa and basis).

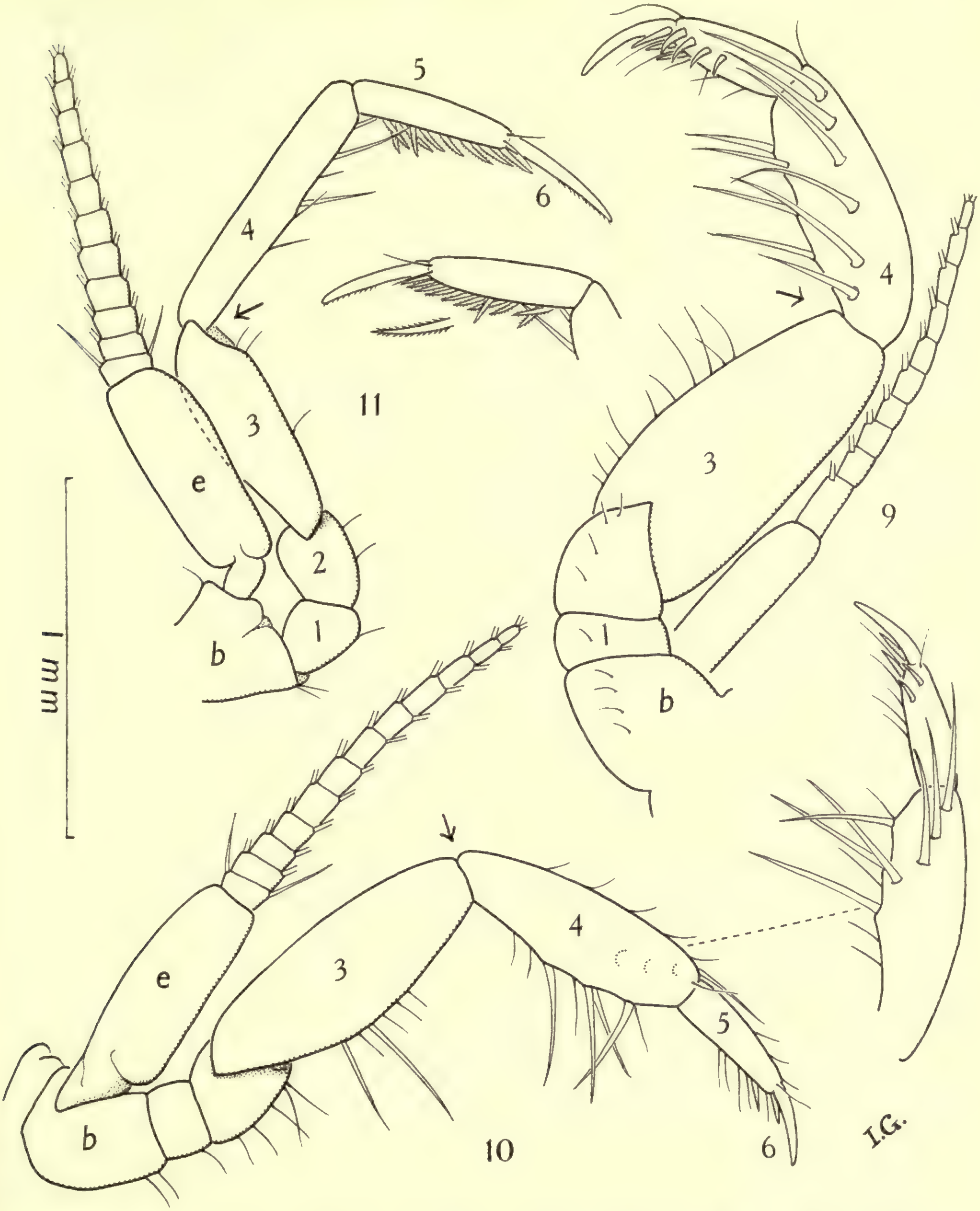
The endopodite—a continuation of the axis of the protopodite—comprises five segments and a strong terminal claw; the "knee" joint between the third and fourth segments is indicated by an arrow. There is a row of strong spines on the inner margin of segments 2 and 3, a group of spines on the distal half of the inner surface of segment 4 and a pair of claw-like spines, flanking the terminal claw, on segment 5. (Since the terminology of the segments of the endopodite varies, I have thought it better in the description of the thoracic limbs to use numbers—see p. 319 for discussion of this).



FIGS. 7 and 8. *Stygiomysis holthuisi* (Gordon). Fig. 7. Right first thoracic limb (maxilliped) of larger paratype. Fig. 8. Posterior part of body of holotype, in ventral aspect. *e*. Exopodite. *b*. Basis. *ep*. Epipodite. *m*. Membranous free lamina connecting and incorporating protopodites of pleopods 5. *t*. Telson. *p*. Backward prolongation of protopodite of uropod. 5 and 6. Fifth and sixth abdominal somites. 3 and 4. Segments of endopodite on either side of "knee" joint (indicated by arrow).

Thoracic appendages 2 to 8. Each of these bears a well developed, natatory exopodite, as in most Mysidacea. All are visible in dorsal aspect, as represented in Pl. 3, each is composed of a long robust proximal segment followed by a more slender tapering flagellum of 10 to 12 segments (Text-figs. 9, 10, 11, *e*). Each segment of the flagellum carries a pair of plumose setae, but only the base of each is inserted in Text-figs. 9–11.

These seven pairs of appendages are arranged in two distinct groups. The three anterior pairs have their endopodites directed forwards, more robust than, and obvi-


5
6
4
11
3
e
2
1
b
1 mm
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3
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10
6
I.G.

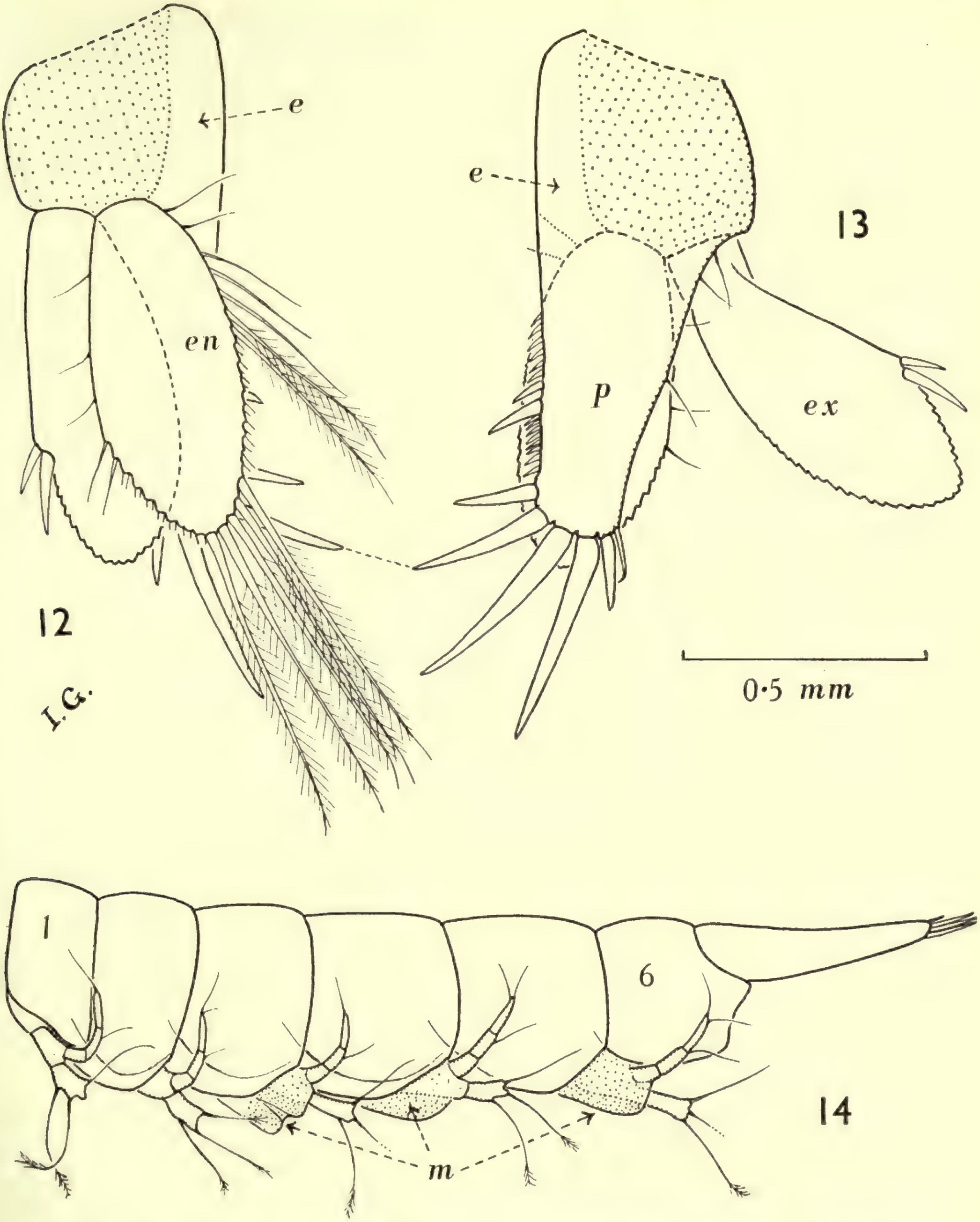
FIGS. 9–11. *Stygiomysis holthuisi* (Gordon). Larger paratype. Fig. 9. Right second thoracic limb (first gnathopod). Fig. 10. Fourth thoracic limb. Fig. 11. Eighth thoracic limb.

b. Basis. *e*. Exopodite. 1 to 6. Segments of endopodite. " Knee " joint indicated by arrow.

ously differing in function from, those of the four posterior pairs which are slender ambulatories. The three anterior pairs should be termed gnathopods since they are probably used to seize prey and pass it to the mouthparts. Thoracic appendages 2, 4 and 8 were removed from the right side of the larger paratype and are represented in Text-figs. 9, 10, and 11 respectively. Appendage 2 is, however, represented in inner, the other two in outer, aspect. The endopodite, beyond the basis which also bears the exopodite (*e*), comprises, as already mentioned in connection with the maxilliped, five segments, or six if the terminal claw is included (Text-fig. 11, *1–6*). The endopodite of gnathopod 1 (thoracic appendage 2) is very robust ; segments 1 and 2 are short, 3 is the longest and by far the broadest, 4 is long and armed with a longitudinal series of six setae on the inner surface and 3 on the ventral margin (with another near the margin), segment 5 is not quite half as long as 4 and is armed with a number of short spines in addition to the terminal claw. Gnathopod 2 (appendage 3) is very similar to, but a trifle less robust than, gnathopod 1 and there are only 4 long setae on the distal half of the inner surface of segment 4. As illustrated in Text-fig. 10, the third gnathopod is much more slender than gnathopod 1, with only three setae on the distal third of the inner surface of segment 4. Thoracic appendages 4 to 8 are all very similar ; they are in fact peraeopods or walking legs, with the endopodite slender as represented in Text-fig. 11. Segment 4 is the longest but segment 5 and the terminal claw are also elongated so that the portion distal to the " knee " is longer than the proximal part. On the ventral margin of segment 5 is a row of curved serrated spines.

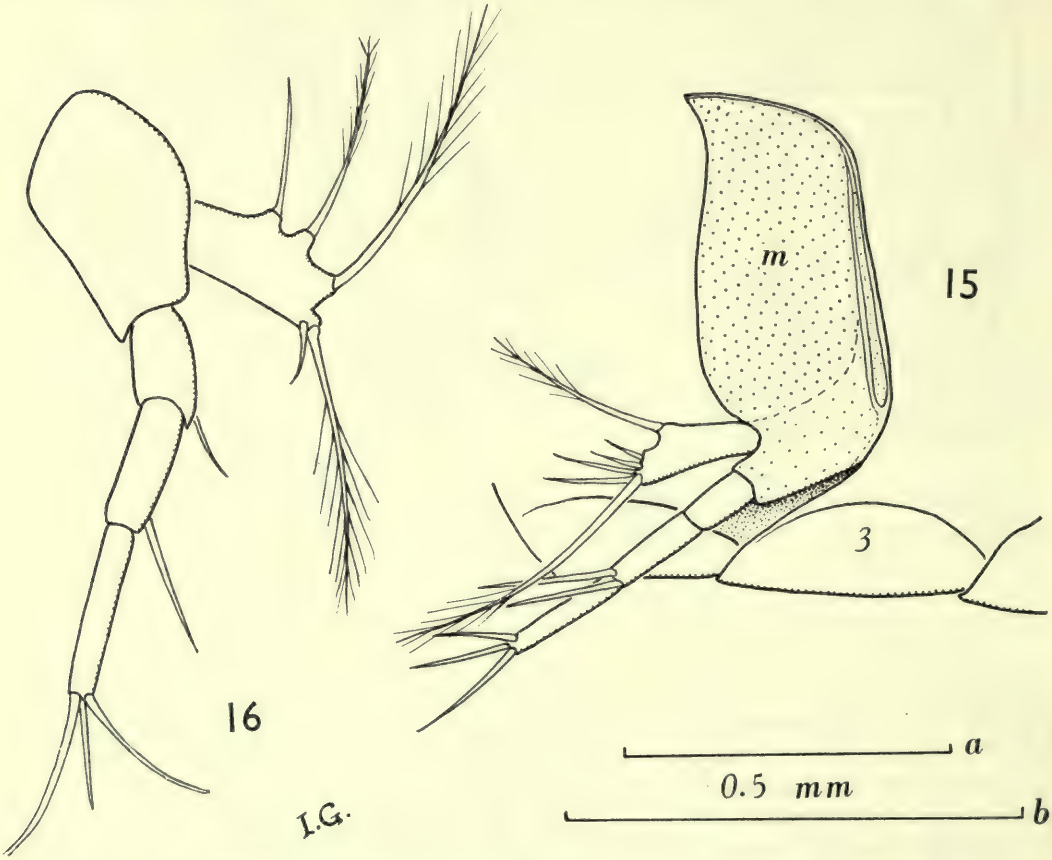
The *pleopods* are similar in form and do not differ much in size from the first to the fifth pairs. Each is a small, biramous appendage comprising a short protopodite, a one-segmented endopodite and a three-segmented exopodite (Text-figs. 8, 14 and 16). The first pair are more widely separated than are any of the others, i.e. they are more laterally placed, so that in dorsal aspect even the endopodites are visible (Pl. 3 and Text-fig. 14) ; in ventral aspect they are concealed by the last pair of thoracic appendages. In other words, abdominal somites 2 to 5 are considerably deeper than somite 1 and their tergites bend in somewhat to meet their respective sternites, thus the pleopods are more ventral in position. A most unusual feature is the presence of a transverse lamella projecting freely backwards from the posterior sternal margin of each abdominal somite 3, 4 and 5. This chitinous duplicature, as Caroli terms it, becomes progressively longer (that on somite 3 being the shortest, that on 5 the longest). The protopodites of each pair of pleopods are incorporated with the respective lamella, but the muscle bands which work the two rami of each pleopod are visible through the chitin (Text-figs. 8, 14 and 15 *m*). Under certain lighting conditions, at a certain angle, there appears to be a median notch (an inverted V) dividing the lamella on somite 3 of the smaller paratype ; when a fine needle point is run along under the free margin of the lamella, however, the posterior margin is found to be continuous.

One of the most distinctive features of this animal is the *uropod* (Text-figs. 8, 12 and 13). The protopodite is expanded medially (*e*), beyond the base of the endopodite (*en*), so that it occupies very nearly half of the posterior margin of the sixth abdominal somite (Text-fig. 8). Moreover, in ventral aspect, it has a long, massive,



FIGS. 12–14. *Stygiomysis holthuisi* (Gordon). Smaller paratype. Fig. 12. Left uropod, in dorsal aspect. Fig. 13. Same, in ventral aspect. The muscle bands within the protopodite are restricted to the stippled area. Fig. 14. Abdomen and telson, in lateral aspect. *e*. Median expansion of protopodite. *en*. Endopodite. *ex*. Exopodite. *m*. Membranous lamellae connecting protopodites of pleopods 3, 4 and 5. *p*. Backward prolongation of protopodite. 1 and 6. First and sixth abdominal somites.

backward prolongation (*p*), which extends almost to the posterior margin of the endopodite and bears five strong apical and subapical spines. These spines curve inwards and upwards (dorsally) towards those on the other partner. On the distal half of the inner margin of *p* there is a row of spinules interrupted by one or two spines. The left uropod of the smaller paratype was removed and is represented, in dorsal and ventral aspects, in Text-figs. 12 and 13. In dorsal aspect only the proximal part of the protopodite with its medial expansion (*e*) is visible. The endopodite conceals part of the exopodite, and the long marginal plumose setae on exopodite and endopodite (mostly omitted in Text-fig. 12) conceal the apical spines on the prolongation *p*. There is no suture line or diaerisis on the exopodite, at the level of the spines on the outer margin, marking off the distal portion. The uropods are unusually stiff (at any rate in fixed specimens); when I tried to spread out the exopodite



FIGS. 15–16. *Stygiomysis holthuisi* (Gordon). Fig. 15. Third left pleopod of female, and left half of membranous lamella, in ventral aspect. Fig. 16. Second pleopod of holotype (female). *m*. Lamella. 3. Side of third abdominal somite. Fig. 16 at larger scale.

from beneath the endopodite it was difficult to do so without damage to the exopodite base (Text-fig. 13 *ex*). There is no statocyst either in the uropod or in the basal segment of the antennular peduncle.

Oostegites. In the holotype there are four pairs of developing oostegites arising from the coxae of thoracic limbs 4 to 7 respectively. The two anterior pairs are equally developed, each partner in the form of a long narrow lamella. The third pair is unequal, the left partner being appreciably larger than the right one ; of the last pair the left one is very small and the right one has not as yet appeared.

NOTE ON THE MALE. On 27th October, 1958 I received from Dr. Holthuis another specimen which had been collected in the type locality on 25th May, 1958 by Mr. M. Vroman. This specimen, which proved to be a male, is rather more slender than the holotype and measures 10 mm. in body length. It is less contracted than the type specimens and not quite so flattened dorsoventrally (Text-fig. 24). The ratio of carapace length to total body length is perhaps more as in the living animal (1 : 4·74 in the male, as against 1 : 3·93 in the holotype). Apart from the more slender build, the presence of short penes, and the sexual dimorphism exhibited by the second pair of pleopods, I find no obvious differences between the male and the holotype—the antennula is often modified in male Mysidacea. Pleopod 2 is represented in Text-fig. 18, that of the holotype in Text-fig. 16. As far as I can see without actually removing one of these pleopods from each specimen, the exopodite is three-segmented in the holotype and only two-segmented in the male. In the latter there are 8 or 9 long, strong, thorny setae (or spines) on the inner margin of the proximal segment and, in addition, 5 to 7 shorter setae which are more oblique (directed more ventrally)—see Text-fig. 18. The first pleopod is represented in Text-fig. 17.

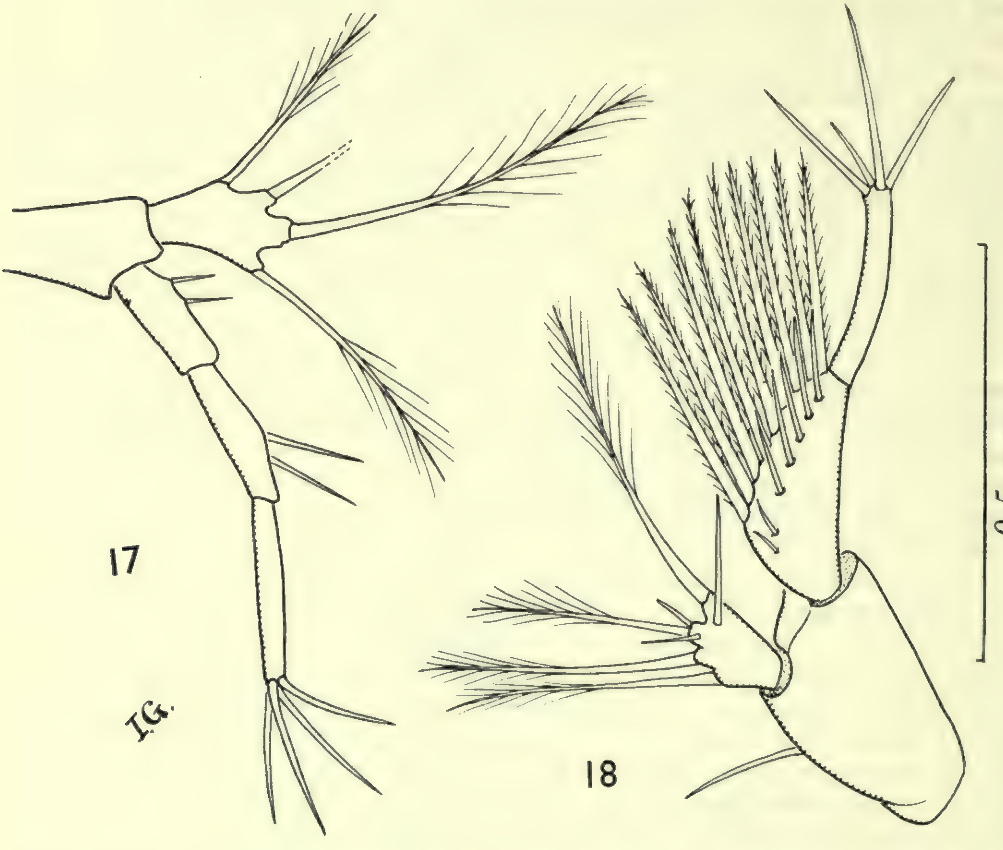
The genital opening is situated on a very low papilla at the base of the last thoracic appendage, on the inner side of the coxa. There is no coxal lamina such as Villalobos (1951, p. 208, Text-fig. 12) has figured for his genus *Typhlolepidomysis*.

REMARKS. These specimens from the West Indies are undoubtedly referable to Caroli's genus *Stygiomysis*, as a comparison of Text-fig. 8 with his Text-fig. 3 (1937, p. 223) shows. The type species of the genus, *S. hydruntina* Caroli, was found in two grottos in the region of Ótranto, Italy (the male holotype in the " Buco dei Diavoli ", one female and two immature specimens in " l'Abisso "). Caroli's brief description, based chiefly on the holotype, makes known the most important characters of the species, and indeed of the genus. As far as I know, the more detailed study which was to have followed (Caroli, 1937, p. 220) has never been published.

In addition to the photograph of the whole animal in lateral aspect, Caroli figured only the first gnathopod (second thoracic appendage) and the posterior end of the body in ventral aspect. Most of his description of *S. hydruntina* would apply equally well to *S. holthuisi*. Nevertheless, the two species differ in certain respects. For example, in *S. holthuisi* segment 5 of the endopodite of gnathopod 1 (that which bears the terminal claw) is much longer than in *S. hydruntina* and the terminal claw and the pair of spines flanking it are very much shorter (in *hydruntina* they are much longer than the segment that bears them—cf. Text-fig. 9 with Caroli, 1937, fig. 2, p. 222). In *S. holthuisi* the terminal claw of peraeopod 4 (last thoracic limb) is rather shorter than segment 5, whereas in *S. hydruntina* the claw is longer than the dactylopodite.

The shape of the uropod differs appreciably in the two species; in *S. hydruntina* the outer margin of the prolongation *p* of the protopodite is distinctly concave, the exopodite is much broader, with a more semicircular apex (cf. Text-figs. 8, 12 and 13 with Caroli, 1937, p. 223, fig. 3).

According to Caroli, the pleopods of the male increase very slightly in length from the first to the fifth pair, but " nessuno di essi mostra particolari modificazioni sessuali ". In *S. holthuisi*, however, the second pair of pleopods in the male are modified; as far as I can ascertain without removing one of these pleopods, the exopodite has only two, instead of the usual three, segments, and the proximal segment has a row of 9 long spines as represented in Text-fig. 18 (compare with the first male pleopod, Text-fig. 17 and with the second female pleopod, Text-fig. 16). Also, the membranous flaps between the third, fourth and fifth pairs of pleopods differ in



Figs. 17–18. *Stygiomysis holthuisi* (Gordon). Male. Fig. 17. First pleopod. Fig. 18. Second (modified) pleopod.

the two species. Caroli says that, in each of these three pairs, " the peduncle (protopodite) is completely fused with a wide duplicature of the integument, in the form of an almost semicircular lamina, movably articulated with the posterior margin of the sternite, [extending] from the external margin to the middle line, where it meets that of the other side " (my translation). He adds that the peduncle proper is indicated by the presence of the muscle bands which work the two rami, but that there is no suture between it and the duplicature (Caroli, 1937, pp. 223–224 and fig. 3). In *S. holthuisi* these duplicatures unite to form a single membranous flap, or lamina in which the muscle bands are visible at either side (Text-figs. 8 and 15). I thought at first that there was a median slit separating the two halves of the membrane of the third pair of pleopods of the smaller paratype of *S. holthuisi*. But, on re-examination, I find that there also the membrane is continuous although it is slightly creased in the middle (Text-fig. 14).

The female specimen of *S. hydruntina* measured only 7 mm. in length, but it also had 4 pairs of developing oostegites arising from thoracic limbs 4–7. These oostegites were probably not quite so well developed as those in the holotype of *S. holthuisi* (*c.l.* = 9 mm.). Caroli is almost certain that the full complement of 7 pairs will be found in *Stygiomysis*. If not, then *Stygiomysis* will be quite exceptional. Seven pairs of oostegites are found in the Lophogastrida (Lophogastridae and Eucopiidae), in the Lepidopidae (all three genera), Petalophthalmidae and Boreomysinae. All the rest of the Mysida (*Thalassomysis* excepted) have only two or three pairs of oostegites arising from the last two or three pairs of thoracic appendages. It is to be hoped that an ovigerous female of either species of *Stygiomysis* will soon be found, so that the exact number of oostegites can be ascertained.

II. ON THE SYSTEMATIC POSITION OF THE STYGIOMYSIDAE

Up to the present time the following cavernicolous Mysidacea have been described or mentioned in the literature :—

STATOCYST ABSENT

Lepidopidae :
- *Lepidops servatus* (Fage) 1924, 1925. Zanzibar.
- *Spelaeomysis bottazzii* Caroli 1924. Italy. (Found a second time by Stammer—see Caroli 1937, p. 226).
- *Typhlolepidomysis quinterensis* Villalobos 1951. Mexico.

Stygiomysidae :
- *Stygiomysis hydruntina* Caroli, 1937. Italy.
- *Stygiomysis holthuisi* (Gordon) 1958. West Indies.

STATOCYST PRESENT

Mysidae :
- *Heteromysis cotti* Calman 1932. Lanzarote.
- *Troglomysis vjetrenicensis* Stammer 1933, 1936. Herzegovina.
- *Antromysis cenotensis* Creaser 1936. Yucatan.
- *Antromysis* sp. Bolivar y Pieltain 1943–44, and 1950. Cuba.

Most of these species occur in fresh or brackish water; *Heteromysis cotti* is a marine species since the cave in which it lives communicates with the sea. (*Antromysis anophelinae* W. M. Tattersall, 1951, p. 230, was discovered in the holes made by a land crab, *Cardisoma crassum* Smith, along with mosquito larvae, far up the mangrove inlets behind Puntarenas, Costa Rica—in water which must have been nearly, if not quite fresh). The cavernicolous species with a statocyst in the endopodite of the uropod are referred to the large family Mysidae, in the suborder Mysida. Those that have no statocyst are peculiar or aberrant in certain respects and their systematic position is less easy to determine. Fage referred the family Lepidopidae to the suborder Mysida while admitting that it had a number of Lophogastrida characters; Caroli thought the family might be regarded as modified or aberrant Lophogastrida and Villalobos thought that it should be placed in a new suborder (see p. 306). Caroli had no hestitation in referring the Stygiomysidae to the suborder Mysida.

GENERAL APPEARANCE. In all three genera referred to the family Lepidopidae (formerly Lepidophthalmidae) the carapace agrees with the accepted definitions of the order Mysidacea. Calman (1909, p. 171), in his definition of the order writes " the carapace extends over the greater part of the thoracic region, but does not coalesce with more than three thoracic somites ". Under morphology lower down on the same page he adds " from five to seven of the thoracic somites are distinct, and the last two or three may be left uncovered by the carapace on the dorsal side ". Calman's definition is adopted by Tattersall, (1951, p. 11) and that given by Zimmer (1927, p. 609) is in agreement with it. It has been altered by Dr. Olive Tattersall to read " *carapace* shield-like, covering the greater part of the thoracic region, fused dorsally with the head region and not more than four anterior somites including the first, which is incorporated in the head " (Tattersall and Tattersall, 1951, p. 11). Dr. Tattersall, in a letter dated 12th November, 1958, informs me that, as far as she can make out, " in some Mysidae there does appear to be fusion of at any rate part of the fourth somite with the carapace (in e.g. *Mysidopsis*, some *Siriella* and in *Neomysis*). I do not know quite how much one can rely on the " saddle " on the carapace in so many mysids, but I always considered it to represent the area of fusion of the two surfaces, i.e. the inner surface of the carapace with the dorsal surface of the thoracic somites involved."

I have examined specimens of *Lepidops servatus* (Fage) but they are delicate and none too well preserved, and it is not easy to discover exactly how many thoracic tergites are free. As in most Mysidacea, the anterior thoracic somites are short and rather crowded together, especially dorsally, and the suture lines are visible laterally. As far as I can see four are certainly free and perhaps five. The last two tergites, which are uncovered by the emarginated carapace, are each as long as the first abdominal somite. The large lateral " wings " of the carapace extend to the first abdominal somite, and can easily be moved away from the body. All three genera retain the " caridoid facies " as do most Mysidacea.

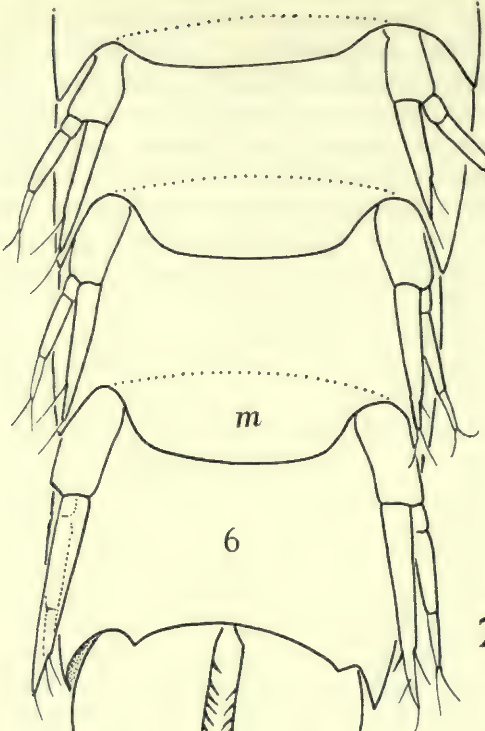
Stygiomysis, on the other hand, does not agree with Calman's definition, even as emended by Dr. Tattersall. The carapace is unmistakably fused with the first four thoracic tergites but has no " wings " to speak of, so that the last four thoracic somites are entirely exposed (Pl. 3, Text-figs. 1 and 24). Moreover, the body behind the short carapace (the sides of which cannot easily be separated from the body—at any rate in preserved specimens) is vermiform and very flexible. Caroli's photograph of *Stygiomysis hydruntina* shows the abdomen curved gracefully upwards, in a most un-mysid-like position (1937, p. 221, fig. 1). As that author says, the short carapace and the apparent division of the thorax into two subtagmata gives the genus "un aspetto particolare". The sixth abdominal somite is distinctly shorter than either the fifth or the fourth somite. In Mysidacea "the sixth abdominal somite is usually longer than any of the others" (Tattersall and Tattersall, 1951, p. 16). This is the chief reason why I at first thought that the genus could not be referred to the order Mysidacea as at present defined (Gordon, 1958).

The other two most striking peculiarities of the genus *Stygiomysis* namely, the transverse membranes with which are incorporated the protopodites of pleopods 3, 4 and 5, and the long backward extension of the protopodite of the uropod, are not quite as unique as I had supposed. Each will be dealt with in turn.

TRANSVERSE CHITINOUS LAMELLAE. Caroli (1937, p. 225) found what he called homologous though not identical structures in *Lepidops* and *Spelaeomysis*. I have been able to confirm his observation in *Lepidops*; between the bases of pleopods 3, 4 and 5 there is a transverse laminar extension from the posterior margin of each abdominal somite, as represented in Text-fig. 20. These chitinous duplicatures of the integument, as Caroli calls them, increase in length from somites 3 to 5 but the protopodites of the pleopods are *not* incorporated with them. In *Spelaeomysis* they are said to be even better developed, with a median emargination in the posterior border. Caroli assumes from this that each lamina had a double origin—i.e. that it arose as two duplicatures of the integument which had fused medially (Caroli, 1937, p. 225, cf. also his fig. 3). Unfortunately, Villalobos (1951) does not state whether or not these laminae are present in *Typhlolepidomysis*; they were overlooked when *Lepidops* and *Spelaeomysis* were first examined and could easily have been overlooked a third time. (But see footnote to p. 308).

Although transverse laminae are known only in these more or less aberrant Mysidacea among the Malacostraca, they recall somewhat analogous structures in the Copepoda. Here it is the thoracic limbs which are involved; "the proximal segments of the protopodites of each pair are connected with each other across the middle line by a plate formed by a transverse fold of the sternal integument . . . so that in the backward and forward movement in swimming the two appendages move as one" (Calman, 1909, p. 81). See, for example, the figures of the reduced last limb of male Harpacticids (P5 ♂) in Chappuis 1931, p. 521, fig. 13; p. 538, fig. 60—these limbs are not always joined in the female.

How do the duplicatures arise in the Mysidacea? In *Lepidops* the chitinous lamina seems to be simply a backward extension or fold of the posterior sternal margin of the abdominal somite, since the protopodites of the pleopods are not involved (Text-fig. 20, *m*). In *Stygiomysis hydruntina*, Caroli's figure (1937, fig. 3) suggests that each lamina may have a double origin—that each half arises as a median expansion of the protopodite of the pleopod which fuses anteriorly with the sternal margin of the abdominal somite, since the two halves merely meet in the



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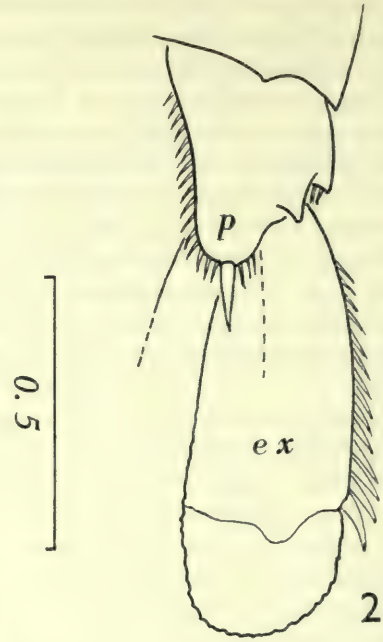

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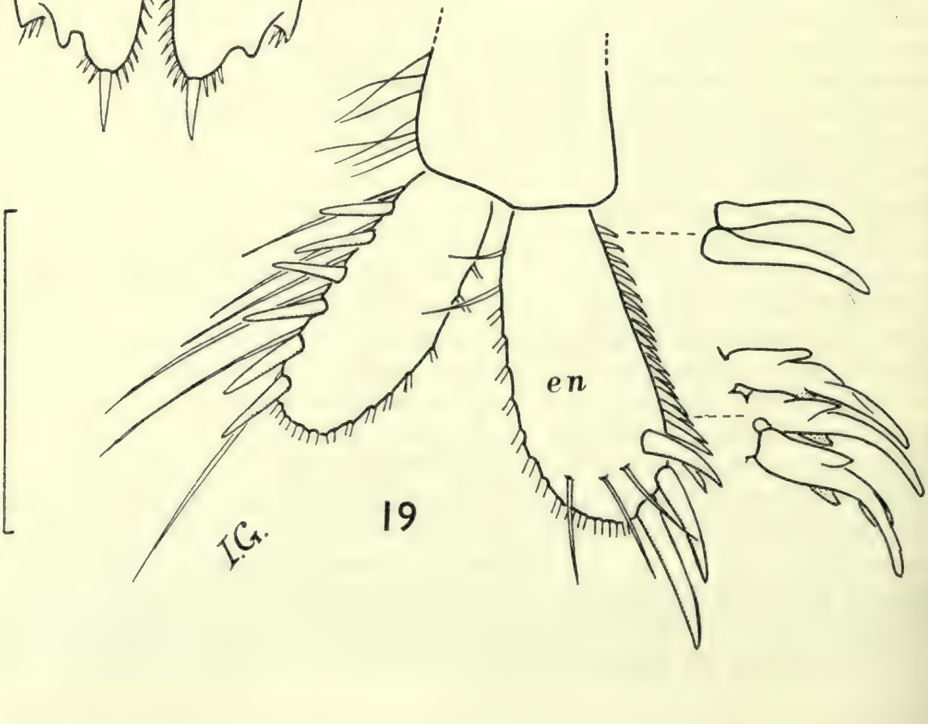

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middle line. In *Stygiomysis holthuisi* the lamina might arise in either of these ways, since the protopodites of the pleopods are incorporated and there is no trace of a median suture line (see also p. 294). It would be interesting to know how these chitinous laminae develop and what their function can be, since the pleopods are almost certainly not natatory. The very thin sternal wall above each lamella may be respiratory,

UROPOD. In *Lepidops servatus* the protopodite is broad, occupying half of the posterior margin of the last abdominal somite. Moreover, on the ventral side, there is a short but distinct backward prolongation armed with a terminal spine and with numerous spinules on the inner border (Text-fig. 21, *p*). This might represent an initial stage in the development of a massive backward prolongation such as is found in *Stygiomysis*, although Caroli prefers to regard it as a last vestige retained in the family Lepidopidae (1937, p. 225). At any rate, this incipient or vestigial structure in *Lepidops* (and presumably also present in *Spelaeomysis*), together with the transverse laminae mentioned above, suggest a fairly close relationship between the Lepidopidae and the Stygiomysidae (see also p. 308). A somewhat analogous structure is characteristic of the uropod of the Stomatopoda, which might indicate that the prolongation of the protopodite is archaic and, as Caroli thinks, may at one time have been much more widely distributed among Malacostraca. I am inclined to think that it is a highly specialized structure which has arisen independently in the Stygiomysidae, and to a lesser extent in the Lepidopidae, in response to some special habit.

It may be mentioned in passing that, in the genus *Micraspides* (Syncarida, Anaspidacea), the uropod is also armed with strong spines, not on the protopodite (which is not prolonged) but on the endopodite. On the dorsal surface, near the posteromedian angle, are three strong spines directed obliquely upwards ; in addition there is a row of special spines on the inner margin (Text-fig. 19, *en*). Nicholls' figure (1931, pl. 32, fig. 15) of the uropod of the type species *Micraspides calmani* is rather small and does not show the row of spines near the external margin of the exopodite. In *Thermosbaena mirabilis* Monod the exopodite of the uropod is remarkably spiny (Monod, 1940, fig. 19).

PLEOPODS. The pleopods of *Stygiomysis*, though smaller and not increasing much in length from the first to the fifth pair, are of the same general form as those of Lepidopidae (Pl. 3, and Text-fig. 14, cf. Text-fig. 20). In both families they are reduced, non-natatory, and biramous *in both sexes*. In *Stygiomysis holthuisi* the second pair is modified in the male although it is not longer than the others (Text-figs. 17 and 18) ; Caroli's statement that there is no sexual dimorphism of the pleopods in

FIGS. 19–21. *Micraspides calmani* Nicholls. Fig. 19. Left uropod of syntype, in dorsal aspect, omitting long marginal setae. *Lepidops servatus* (Fage). Syntype from Paris Museum. Fig. 20. Abdominal somites 3 to 6, and protopodites of uropods, in ventral aspect, showing membranous free laminae (*m*) on posterior margin of somite 3, 4 and 5, between bases of the pleopods. Fig. 21. Left uropod, in ventral aspect (endopodite damaged). *en*. endopodite. *ex*. Exopodite. *p*. Short backward prolongation of protopodite. Scale = 0·5 mm.

S. hydruntina requires corroboration. The second pleopod of the male is similarly modified in all three genera of the Lepidopidae—see Fage, 1925, fig. VI, 2 and 2 ♂; Caroli 1924, p. 513; Villalobos 1951, fig. 13, A and B. (A glance at fig. 1 of Villalobos' paper shows that pleopod 2 is shorter than pleopod 5 in the male holotype; it seems, therefore, that in his fig. 13, C and D are drawn at a smaller scale than A and B). Pseudobranchiae are absent in both Stygiomysidae and Lepidopidae.

In Lophogastrida the pleopods of both sexes are well developed, biramous, multisegmented and natatory; they may be considerably larger in the male than in the female, but are unmodified or very slightly so. In Mysida they are seldom alike in both sexes and generally exhibit marked sexual dimorphism. In the female they are, as a rule, rudimentary, uniramous (rarely the first may be biramous) and non-natatory; occasionally those of the male are all rudimentary as in the female (*Mysidella, Mysidetes, Heteromysis*). In the male they are sometimes biramous, natatory and unmodified (Petalophthalmidae), or the third, or second and third, pairs are slightly modified (Boreomysinae); more often one or more pairs are reduced as in the female and one or more pairs are modified as accessory copulatory organs; pseudobranchiae are present. The pleopods which are most commonly modified are the third and/or fourth pairs. In the genus *Rhopalophthalmus* it is the second pair (Tattersall, O.S. 1957, fig. 7H, compare with G, J, K and L); but here the pleopods are biramous, multiarticulate, with conspicuous pseudobranchial lobes at the bases of the endopodites. The modified pair, or pairs, of male pleopods are usually long and conspicuous in the family Mysidae, to which *Rhopalophthalmus* belongs. It is just a coincidence that the same pair of male pleopods is modified in this genus as in the cavernicolous families under discussion.

MOUTHPARTS. There are numerous differences in detail between the individual mouthparts of the two families and these are doubtless correlated with differences in feeding habits. For example, in the Lepidopidae the molar process of the mandible is better developed, the palp is larger and the second and third segments are each armed with a close row of thorny spines (cf. Text-fig. 27, where many of the spines and setae are omitted, Fage, 1925, fig. IV, *M* and Villalobos, 1951, fig. 6 with figs. 4 and 5).

According to Tattersall and Tattersall, (1951, pp. 20–21), in Mysidacea the maxillula is smaller than the maxilla and always lacks a backwardly directed palp or endopodite except in the genus *Gnathophausia*. This statement requires amplification however, because there is a palp in all three genera of the Lepidopidae (Fage, 1925, fig. IV, m^1; Caroli, 1924, p. 513 and Villalobos, 1951, fig. 7). In each of three specimens of *Lepidops servatus* which I have examined, this palp has a median constriction and appears, therefore, to be two-segmented as in *Typhlolepidomysis* (see Text-figs. 27 and 28). Moreover, in *Stygiomysis holthuisi* the maxillula is larger than the maxilla; the outer endite is stout and one of its apical spines is greatly enlarged; there is no palp (Text-figs. 2 and 5; cf. the small maxillula of *Lepidops* represented in Text-figs. 28 and 27).

The maxilla of *Stygiomysis* has strong spines rather than setae on the whole inner margin but they do not continue along the lower border of the simple endite (Text-fig. 6, on *en*, *d* and *s*); in the Lepidopidae the inner and lower margins of the maxilla bear numerous finer setae and spines, and the segments of the endopodite are much longer (Fage, 1925, fig. IV, m^2 and Villalobos, 1951, fig. 8). The first thoracic appendage or maxilliped of *Stygiomysis* is more pediform, lacks the large endites, but has strong spines on the inner margin of the distal segments of the endopodite (Text-fig. 7; cf. Fage, 1925, fig. VI, *mp* and Villalobos, 1951, fig. 9). According to Siewing (1958, pp. 250–251) this appendage should be called a gnathopod in the Stygiomysidae and a maxilliped in the family Lepidopidae (see later, under terminology, p. 316). Differences such as these may be found between closely related families of Mysidacea. The exopodite of the first thoracic limb is reduced to a simple unsegmented lamina, which is relatively smaller in *Stygiomysis holthuisi* than in either *Lepidops* or *Typhlolepidomysis* (cf. Text-fig. 7 with Fage, 1925, fig. VI, *mp* and Villalobos, 1951, fig. 9). In this respect both families are nearer to the suborder Lophogastrida and to the Petalophthalmidae (in which the exopodite is lacking, as in some species of *Gnathophausia*) than to the Mysidae.

LABIUM. The paragnatha in *Stygiomysis* are unusual and very conspicuous, although Caroli did not mention them. To discuss the labium at this point would necessitate rather a lengthy digression; it will be dealt with in a separate section later on (p. 309). Of the paragnatha that I have examined, those of *Lepidops* seem to be nearest to those of *Stygiomysis*.

THORACIC APPENDAGES 2–4. Many of the peculiarities of the mouthparts mentioned above are doubtless correlated with the fact that in Stygiomysidae three pairs of thoracic appendages (2–4) are modified as gnathopods, whereas in Lepidopidae only one pair, the second, is thus modified (cf. Pl. 3, Text-figs. 9 and 10 with Fage 1925, fig. V, p^2 and Villalobos, 1951, fig. 10). Incidentally, Villalobos refers to the second thoracic limb as " primer par de pereiópodos " in the text and as " maxilipedo del secundo par " in the legend to fig. 10 and Caroli (1937, p. 226) says " toracopodi 2–4 (gnathopodi) massillipediformi "! Only in the family Eucopiidae of the suborder Lophogastrida are the same three pairs of thoracic limbs modified as gnathopods; but in this family the following three pairs of appendages are elongated and specially modified (Tattersall and Tattersall, 1951, p. 111, figs. 13C, D and E and 12A). When Sars (1885, p. 59) suggested that the long prehensile thoracic limbs 5 to 7 might be used for seizing hold of Hydroids or Crinoids fixed at the sea bottom, he was unaware of the fact that the Eucopias are bathypelagic (Fage, 1941, p. 3 and 1942 pp. 3 and 60). There is nothing in mid-water for a bathypelagic animal to cling to; these prehensile endopodites, reaching well beyond the body, seem admirably suited for keeping the animal suspended and for seizing prey which could be passed to the short robust endopodites of the gnathopods (see p. 319). *Stygiomysis* is probably raptorial in its feeding habits whereas the Lepidopidae are probably predominantly filter feeders.

OOSTEGITES. In Lophogastrida, Lepidopidae, Petalophthalmidae and Boreomysinae (Mysidae) a pair of oostegites or brood lamellae arises from each pair of thoracic appendages 2–8. Throughout the rest of the large family Mysidae there are either three or two pairs, arising from the last three or two pairs of thoracic appendages. The only exception to this rule is the genus *Thalassomysis* Tattersall 1939, p. 238 (established two years after Caroli's genus *Stygiomysis*). Here reduction has not gone quite as far and four pairs of oostegites are present. Of these the first pair is vestigial, the second pair small and the last two pairs form the major part of the brood chamber. Oostegites disappear from the more anterior limbs first so that, no matter what their number, a pair is always present on the seventh and the eighth thoracic appendages. In *Stygiomysis* the full complement is unknown but, unless the genus is quite exceptional, there ought to be a pair on the eighth thoracic limbs ; this means that there ought to be at least five pairs and Caroli may be right in thinking that there may be seven pairs.

DISCUSSION. The family Stygiomysidae seems to be distinct from, but most closely related to, the family Lepidopidae. But, as already mentioned, opinion differs as to the systematic position of the family Lepidopidae. Since gills are absent and the pleopods are reduced, non-natatory, Fage (1924, 1925) referred his new family " Lepidophthalmidae " to the sub-order Mysida (Mysidea of some authors), at the same time stressing its affinities with the sub-order Lophogastrida. Both Caroli and Villalobos have raised objections to this. Caroli's announcement of *Spelaeomysis* appeared before Fage's main paper (in December, 1924). He says that the discovery of a second genus in Italy, so far from the habitat of the first genus (Zanzibar), shows that these forms must have had at one time a very wide distribution. " Però è forse prematuro ritenerle come forme di passagio dai *Lophogastrida* ai *Mysida*. A mio avviso, potrebbero anche essere considerate *Lophogastrida* modificati (perdite delle branchie, riduzione dei pleopodi) dalla vita cavernicola assunta in epocha remota " (Caroli, 1924, p. 513). That Fage adheres to his original opinion is evident from a remark he makes in a later work on Lophogastrida (1941, p. 3) ; discussing some primitive characters he mentions " le palpe retroversé, hérité des Cumacés et des Tanaidacés, que portent au premières maxillae les *Gnathophausia*. Seuls parmi les Mysidés [Mysida] les genres *Lepidops* (*Lepidophthalmus* Fage 1924) et *Spelaeomysis* Caroli 1924 en sout pourvus, qui révèlent ainsi leur part du meme héritage ". Villalobos (1951, p. 216), after a brief discussion of the systematic position of the Lepidopidae concludes : " Según nuestro punto de vista, la posición adoptada por Fage es un poco forzada, porque si los caracteres distinctivos de la familia se encuentran representados ya sea en *Lophogastridea* o en *Mysidea*, lo conveniente seria crear un soborden intermedio ". He did not, however, propose a new sub-order because of the paucity of material and the small number of genera and species known (three monotypic genera).

When Caroli (1937, p. 225) discovered the transverse lamellae and a short but distinct backward prolongation of the protopodite of the uropod in *Lepidops* and *Spelaeomysis* (see Text-fig. 20, *m* and Text-fig. 21, *p* of this paper) he said that he could not judge whether the presence of these two characters indicated a closer affinity between the Lepidopidae and *Stygiomysis*. " Si puŏ anche suppore che si trata di caratteri arcaica, communi probabilmente in passato ad altre e più numerose forme, e conservatisti, benché in via di graduale riduzione, nei nostri Misidacei, in grazzia dello speciale *habitat* ". He does not explicitly say that he has altered his earlier opinion (1924) namely, that the Lepidopidae are perhaps modified Lophogastrida, and he has no hesitation in referring the Stygiomysidae to the sub-order Mysida.

The family Lepidopidae shares its diagnostic characters with the rest of the Mysidacea as follows :—

(i) Gills absent : Stygiomysidae and the whole of the Mysida.

(ii) Oostegites seven pairs : Lophogastrida, Petalophthalmidae, Boreomysinae and ? Stygiomysidae.

(iii) Statocyst absent : Lophogastrida, Stygiomysidae and Petalophthalmidae.

(iv) Palp present on maxillula : *Gnathophausia* only (Lophogastrida).

(v) Exopodite of maxilliped (first thoracic limb) a small unsegmented lamella or absent : Lophogastrida, Stygiomysidae and Petalophthalmidae.

(vi) Second thoracic appendage modified as a gnathopod : most Lophogastrida and Mysida—in the Stygiomysidae and Eucopiidae the next two pairs are similarly modified.

(vii) Endopodites of thoracic appendages 3–8 (or 5–8) without subdivision of the penultimate segments : Lophogastrida, Stygiomysidae, Petalophthalmidae and a few Mysidae.

(viii) Pleopods reduced, non-natatory, but biramous in *both* sexes ; second pair slightly modified in ♂ ; Stygiomysidae (see p. 303).

(ix) Transverse lamellae arising from the posterior sternal margins of abdominal somites 3, 4 and 5 ; Stygiomysidae, though here the protopodites of the pleopods are also incorporated in the lamellae. (Text-figs. 20 and 8 and Caroli, 1937, fig. 3).

(x) A short but distinct backward prolongation of the protopodite of the uropod : Stygiomysidae, here it is very much longer (Text-figs. 21 and 13, *p*).

(xi) Exopodite of second thoracic limb normal, multiarticulate : most Mysidacea (except *Petalophthalmus*, where it is absent). It is long and natatory as in forms with reduced pleopods. The basal segment of this and the following exopodites are long and narrow as in *Stygiomysis* and Lophogastrida, not blade-like as in most Mysida.

Certain characters mentioned by Fage in his diagnosis of the family Lepidopidae are of less importance in trying to elucidate affinities since they may vary within one and the same family : (*a*) Endites or lobes on the first thoracic endopodite may be large, poorly developed or absent, depending on the feeding habits. They are well developed in all three genera of Lepidopidae, absent in Stygiomysidae ; in the family Mysidae they are large in *Mysis*, one only is present in *Mysidetes* and they are absent in *Mysidopsis*. In the Petalophthalmidae they are absent in *Hansenomysis*, present in *Petalophthalmus*. In the Lophogastridae they are present in *Gnathophausia* (Text-figs. 33–34), absent in *Lophogaster*. (*b*) Presence or absence of a suture line (diaerisis) on the exopodite of the uropod. In the Lepidopidae there is one in *Lepidops* (which only shows up well in reflected light) ; it is said to be present in *Typhlolepidomysis*, absent in *Spelaeomysis*. It is present in the majority of the Lophogastrida and in Petalophthalmidae, is faint and incomplete in Siriellinae, absent in other subfamilies of Mysidae and in Stygiomysidae. *Rholapophthalmus* is exceptional in having a suture in both exopodite and endopodite.

From the above general survey of the characters used to subdivide the order Mysidacea, it is obvious that, as far as external morphology is concerned, the only constant character separating the Lophogastrida from the Mysida, Lepidopidae and Stygiomysidae, is the presence of podobranchiae or gills on some or all of the thoracic limbs. A negative character like the absence of gills does not necessarily imply that the Lepidopidae and the Stygiomysidae belong to the Mysida—as Caroli 1924, p. 513 implies, loss of gills may have occurred more than once in the course of evolution. Several of the Lophogastrid characters are shared by the Lepidopidae, Stygiomysidae and Petalophthalmidae and the large number of oostegites is shared by the Boreomysinae also (as are natatory pleopods in the male). But I do not see that anything is to be gained by erecting a third suborder for the Lepidopidae and Stygiomysidae. In that case something would have to be done about the Petalophthalmidae and perhaps the Boreomysinae as well. In the meantime, I prefer to leave both families (Lepidopidae and Stygiomysidae) in the Mysida since podobranchiae are absent and the pleopods are reduced. These two families are very closely related to each other and differ in several important characters from the rest of the Mysida—the similar pleopods, the transverse lamellae on abdominal somites 3, 4 and 5 and the greater or lesser prolongation of the protopodite of the uropod. Their relationship to each is much the same as that of the Lophogastridae and Eucopiidae. Whatever future specialists may decide to do with the Lepidopidae, I am convinced that the Stygiomysidae should be ranked along with it—even if there should be fewer than seven pairs of oostegites in *Stygiomysis*.

The family Lepidopidae requires redefinition, because certain characters were overlooked at first ; also for comparison with that of the Stygiomysidae, which is the same as for the genus *Stygiomysis* (see p. 286).

DIAGNOSIS OF THE FAMILY LEPIDOPIDAE : Cavernicolous Mysidacea exhibiting the "caridoid facies". Carapace relatively long, smooth or with a sinuous furrow ; produced antero-laterally beyond the rounded rostral margin, postero-lateral "wings" well developed, reaching the first abdominal somite laterally, but leaving the last two thoracic tergites exposed dorsally. (A scale-like process on penultimate thoracic tergite in *Typhlolepidomysis*)[1]. Abdomen, including telson, half as long again as the cephalothorax, not broader in middle, sixth somite as long as, or longer than, fifth. Telson truncate or tapering ; spinules or spines on distal half of each lateral margin as well as on the rounded apex (spinulation not mentioned in *Spelaeomysis*). Ocular scales quadrangular, distal margin oblique, without or with traces of visual elements (a few ommatidia in *Lepidops*). Antennular and antennal flagella as long as (*Lepidops*), or far exceeding, the length of the body (*Typhlolepidomysis*)[1] ; antennal scale well developed, with setae on inner and outer margins. Labrum oval, longer than wide (*Lepidops*). Labium with paragnatha well separated proximally, but not as long as in Stygiomysidae. Mandible with well developed incisor and molar processes ; a row of strong thorny spines on second and third segments of the palp. Maxillula small, with a 2-segmented reflexed palp ending in a long curved

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[1] Since this paper went to press I have collected specimens of *Spelaeomysis bottazzii* from the type locality. It has enormously long antennae and a scale behind the dorsal posterior emargination of the carapace. *Typhlolepidomysis* is therefore a synonym of *Spelaeomysis*. 24.xi.59.

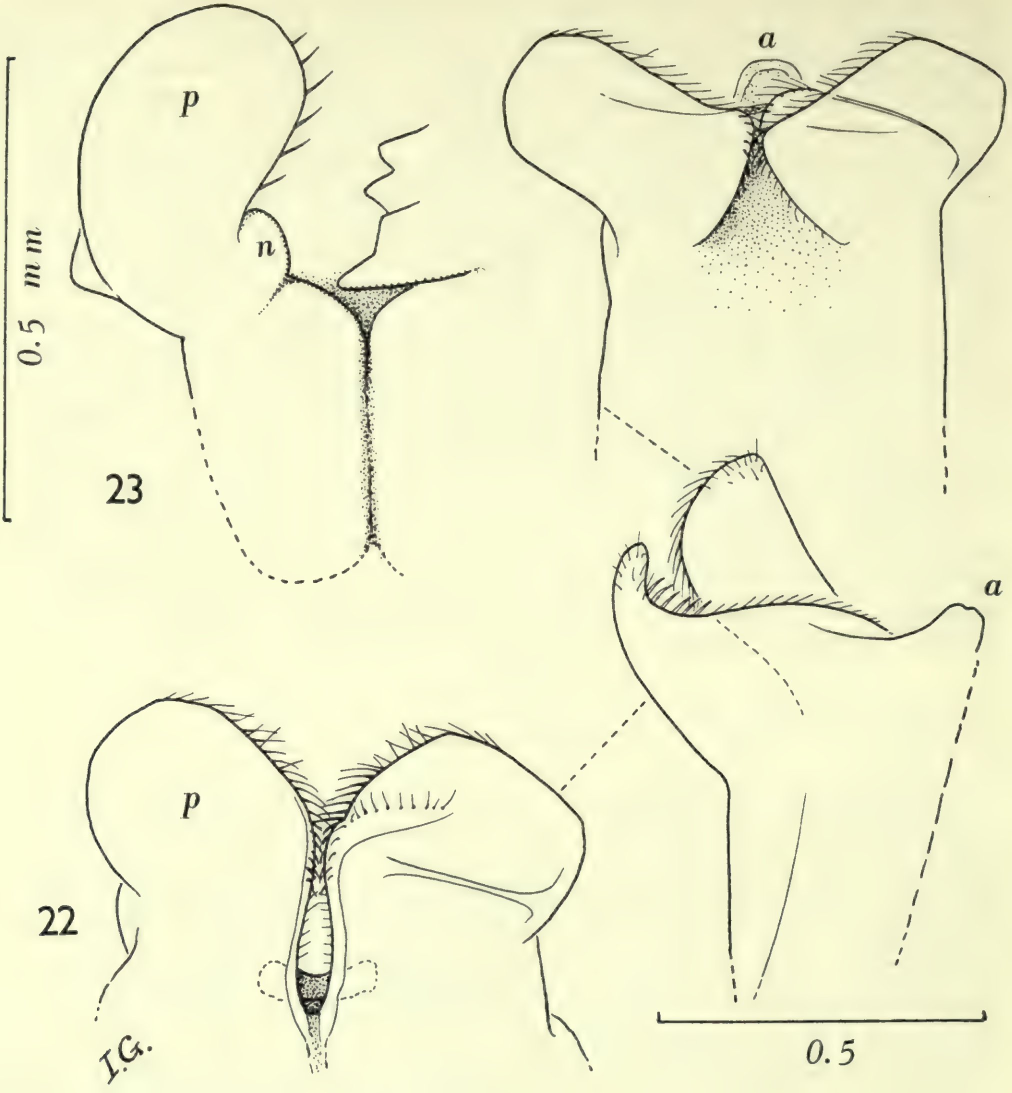
seta; all apical spines on the distal endite of about same size. Maxilla with setae, some of which are distally plumose; segments of endopodite quite long. Maxilliped not pediform, with well developed endites and the penultimate segment broadened; exopodite a small unsegmented lamella with or without fine marginal setules; epipodite rather long and narrow. Second thoracic appendage with exopodite longer than endopodite, which may be modified as a gnathopod. Thoracic endopodites 3 to 8 all slender ambulatories. Penultimate segments of thoracic endopodites not subdivided. Pleopods alike in both sexes, apart from the slight sexual dimorphism exhibited by the second pair; they increase in size from the first to the fifth pair, are biramous, with one-segmented endopodite and three-segmented exopodite (four-segmented in the second pair in the female). A short but distinct transverse chitinous lamella projects from the posterior sternal margin of abdominal somites 3, 4 and 5, with which the protopodites of the pleopods are *not* incorporated. Uropod with a small but distinct backward prolongation of the protopodite, armed with a terminal spine (? overlooked in *Typhlolepidomysis*); statocyst absent; a sinuous suture line on the exopodite (absent in *Spelaeomysis*). Seven pairs of oostegites.

Type genus: *Lepidops* (Fage) 1924, 1925. *L. servatus* (Fage) is stated to be planktonic: " il existait dans ce petit lac de Machumwi-Ndogo un véritable plancton, composé de petits Schizopodes à yeux tres réduits. Ils ne se sont pas fait prendre aux nasses, mais nous en avons receuilli un grand nombre pres de la surface, au filet fin ". Allaud et Jeannel in Jeannel and Racovitza (1914, p. 381).

III. NOTE ON THE PARAGNATHA IN SOME MYSIDACEA

As a rule, little or no attention is given to the labium or lower lip when the mouthparts of Malacostraca are examined—unless, of course, the feeding habits are being studied in detail. It is scarcely surprising, therefore, that in the subject index of the Ray Society Monograph of the British Mysidacea (Tattersall & Tattersall, 1951) the labrum or upper lip is included, but the labium is not mentioned under any of its synonyms (hypostoma, metastoma, paragnatha). In *Stygiomysis*, however, the paragnatha are so conspicuous that they could not possibly be overlooked (Text-figs. 1 and 3, *l* and Text-fig. 23, *p*); yet Caroli does not mention them in his description of *S. hydruntina* (1937).

Michael Sars (1862, pl. 1, figs. 25 and 26) gave two minute sketches of the labium of *Lophogaster typicus* and G. O. Sars not infrequently figured the posterior, as well as the anterior lip. In his *Challenger* Report for example, he included small figures of the labium of *Gnathophausia* and *Eucopia* (Lophogastrida), of *Anchialus* and *Euchaetomera* (Mysida) (Sars, 1885, pl. 8, fig. 5; pl. 9, fig. 8; pl. 34, fig. 11; pl. 35, fig. 7 and pl. 37, fig. 5). These suggest that the labium is more deeply cleft in the Mysida than in Lophogastrida. The paragnatha are also figured *in situ* for *Hemimysis* by Cannon and Manton (1927, pl. III, fig. 4) and for *Lophogaster* by Manton (1928, pl. III, fig. 6); and there are others. But I do not recall having seen any illustration of the paragnatha quite like those of *Stygiomysis*. In lateral aspect, they are unusually pendant, falling well below the level of the labrum, and the distal part of each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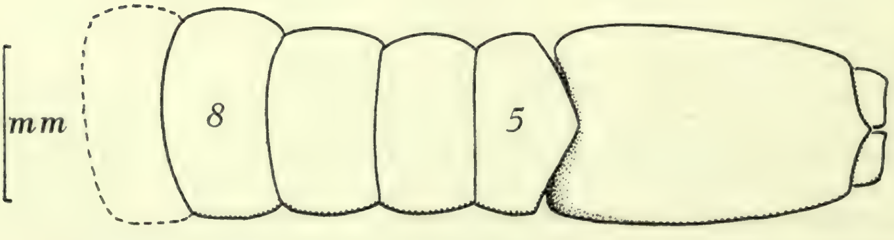

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is spoon-shaped. (Text-fig. 1, *l*). In ventral aspect, the paragnatha are widely separated proximally, and the spoon-shaped parts conceal much of the mandibles and may over-reach the posterior rim of the labrum (Text-fig. 3, *l* and Text-fig. 23, *p*). I am not sure whether there is a subsidiary basal lobule or whether it is just a twist to form a sort of neck (*n*) or stalk for the spoon-like head. I have examined the paragnatha in several genera of Mysidacea for comparison with those of *Stygiomysis*. But there is far more variation than I had anticipated and time is lacking for a detailed comparative study. Nouvel (1943) made a very careful study of the labrum in most of the species that he described and figured in his excellent Report. But, as a rule, he does not mention the labium except in *Thalassomysis tattersalli* in which he says that it is " trés aberrant. Il est aussi très proeminent et asymétrique. Sa partie droite distale [right paragnath] comporte une cavité où vient se loger la dent du labrum. Sa partie gauche épouse aussi le contour du bord postérieur gauche du labrum. Presque toute la partie distale est couverte de petites soies analogues à celles du bord gauche du labrum " (p. 59 ; pl. III, fig. 89). But he does not say what he considers the most typical form, or forms, of the labium in the Mysidacea.

In *Eucopia sculpticauda* Faxon (Eucopiidae–Lophogastrida) the labium, represented in Text-fig. 32, is not quite as deeply cleft as that of *Lophogaster* (Lophogastridae) as figured by M. Sars (1862, pl. 1, fig. 25) ; in the micro-preparation the paragnatha are slightly displaced, owing to pressure of the cover slip, so that a secondary lobule, armed with marginal spinules, is visible (cf. *Lophogaster* in Manton, 1928, pl. III, fig. 6).

Of the highly specialized yet primitive family Petalophthalmidae (Mysida) I have examined *Petalophthalmus armiger* W. Suhm and *Hansenomysis fyllae* (Hansen). In *Petalophthalmus* the labium is deeply cleft (Text-fig. 26, right-hand drawing) ; in ventral aspect, the paragnatha are much longer than wide, are separated proximally by a narrow gap and meet distally. In lateral aspect, each paragnath is deeply concave, almost bowl-shaped, and the cutting edge of the mandible lies in the concavity (Text-fig. 26, left sketch, *l* and *m*). In *Hansenomysis* the paragnatha are also longer than broad and *in situ* are not widely separated proximally (Text-fig. 29, upper sketch, made before mounting on a micro-slide). In the micro-preparation the paragnatha are displaced owing to pressure of the cover-slip and the inner lobules with their marginal spinules are visible (cf. Text-figs. 29 and 32).

In Text-fig. 22 the labium of *Boreomysis rostrata* Illig (Boreomysinae-Mysida) is represented in three different aspects ; the paragnatha are slightly asymmetrical and there is no distinct subsidiary lobule on either of them. An inner knob or boss (*a*) can be seen *in situ* between the paragnatha (upper right sketch which is the aspect

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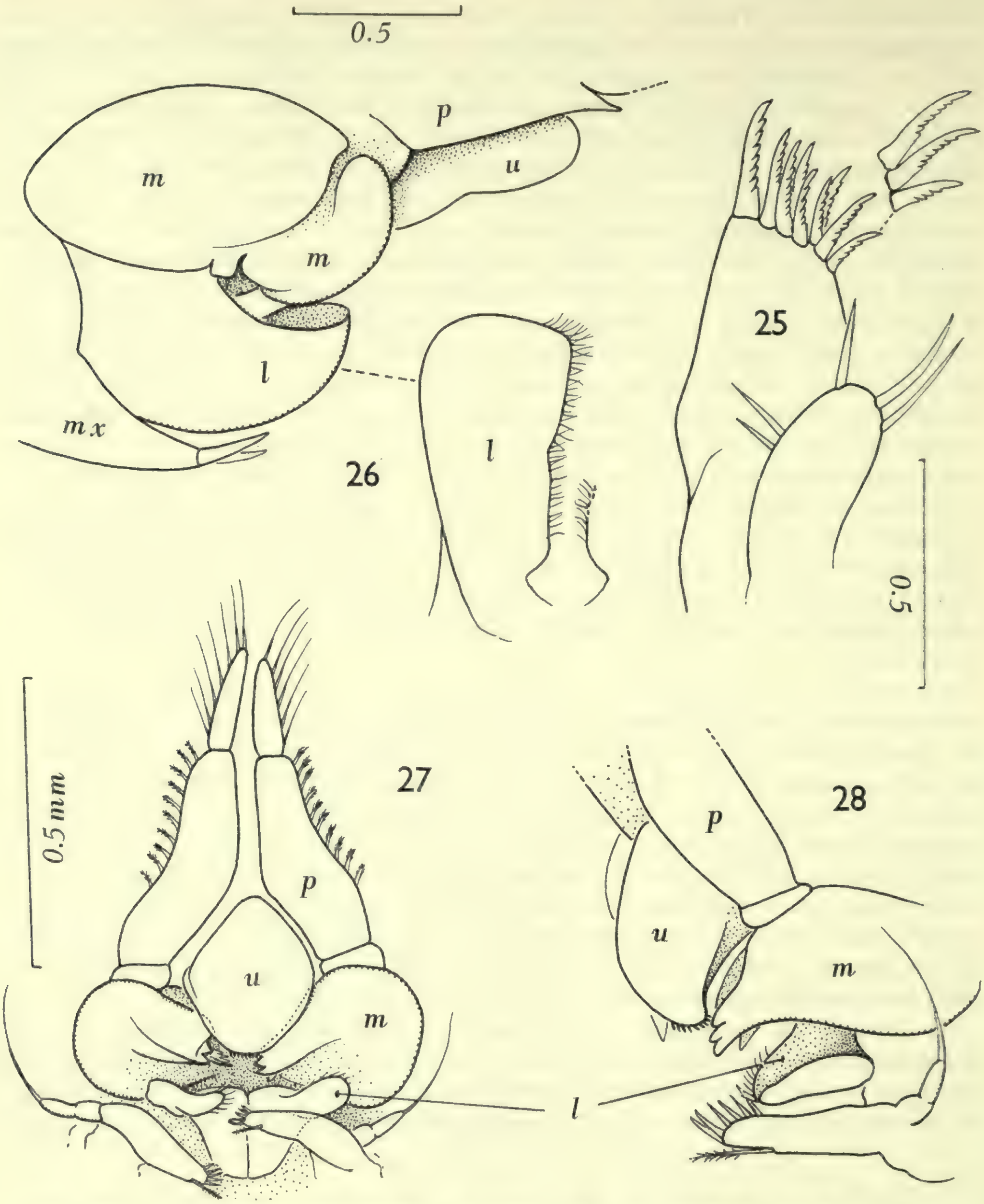
FIGS. 22–24. *Boreomysis rostrata* Illig. Fig. 22. Labium or lower lip, in three different aspects. *Stygiomysis holthuisi* (Gordon). Fig. 23. Right half of labium, in ventral aspect (incisor edge of left mandible also shown). Fig. 24. Anterior half of male, in dorsal aspect. (first abdominal somite represented by broken line). *a*. Boss on labium. *n*. Neck. *p*. Paragnath. 5 and 8. Fifth and eighth thoracic somites.

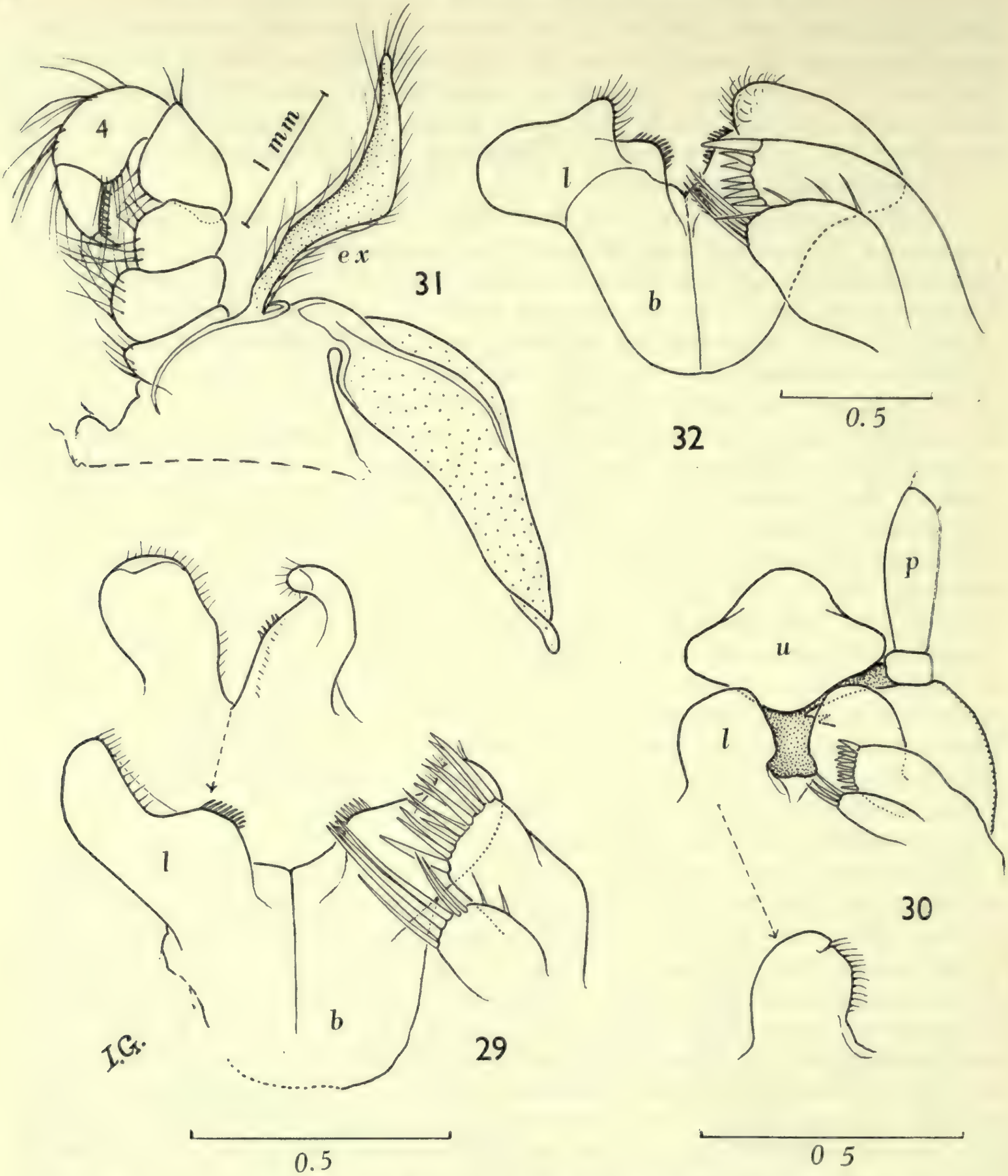


FIGS. 25–28. *Petalophthalmus armiger* W. Suhm. (Reg. no. 1940,viii.5. 568–569). Fig. 25. Right maxillula. Fig. 26. Labrum, right mandible, paragnath and maxillula, in lateral aspect; also right paragnath in ventral aspect. *Lepidops servatus* (Fage). Syntype from Paris Museum. Fig. 27. Labrum, labium, mandibles and maxillulae, in ventral aspect. Fig. 28. Same, in lateral aspect, at higher magnification. *l*. Paragnath of labium. *m*. Mandible. *mx*. Maxillula. *p*. Mandibular palp. *u*. Labrum or upper lip.

from which most other paragnatha are figured). In the micro-preparation of *Indomysis annandalei* Tattersall (Mysini–Mysida) the labrum and labium are somewhat flattened by the cover-slip (Text-fig. 30, upper sketch) ; the labium is more deeply cleft than in *Eucopia* (Text-fig. 32) ; each paragnath is almost as wide as long and may touch the posterior margin of the labrum ; there is apparently no secondary lobule (upper and lower sketches).

Of *Lepidops servatus* (Fage), which is a very minute and fragile species, I have examined a damaged specimen in which the paragnatha are flexed away from the mandibles and the right maxillula is somewhat displaced. The camera lucida sketches were prepared before any attempt was made to mount the fragment (Text-figs. 27 and 28). The paragnatha are obviously rather widely separated proximally and, of all those examined, they approach most nearly to those of *Stygiomysis* although they are smaller and have no " neck " portion (or subsidiary lobule—see p. 311). In my preliminary note on " *Rhopalonurus* " *holthuisi* I referred to the paragnath or main lobe as a lappet (Gordon, 1958, p. 152) but it probably is *not* comparable with the small moveably articulated lappets found in some Tanaidacea. The proximal portion (Text-fig. 23, *n*) may represent the subsidiary lobule which is present in *Eucopia* and in *Hansenomysis* (Text-figs. 32 and 29—in each the lobule is beset with spinules)—or it may just be the result of a slight twist to form a " neck " or stalk. The unusual form and size of the paragnatha in *Stygiomysis* is probably a secondary specialization connected with its feeding habits, as are the other peculiarities of the mouthparts. The *large* maxillula with the remarkably enlarged spine on the distal endite has already been referred to ; I have figured the maxillula of most of the species of Mysidacea examined for comparison with that of *Stygiomysis* (cf. Text-figs 25–28 and 29, 30, 32 with Text-figs. 3 and 5). When the anterior (uppermost) spine on the distal endite is larger than the others this difference in size is not very pronounced (Text-figs. 25, 32 and 30).

The feeding habits have been studied in detail only in a few species of Mysidacea although they have been deduced or inferred from an examination of the mouthparts in other species. But the significance of the marked differences in both form and size of the paragnatha, for example, is not known. A summary of our knowledge of food and feeding habits is given in Tattersall & Tattersall, 1951, pp. 29–33 and other references are listed in their subject index under feeding habits, food, filter feeding and raptorial feeding. Many Mysids employ the filtratory method and the raptatory method quite independently, e.g. *Hemimysis* (Cannon and Manton, 1927) and *Gnathophausia*, although in the latter there can be no auxilliary food current created by the thoracic exopodites as in other primitive filtratory Malacostraca (see Manton, 1928, p. 117). Others are incapable of filter feeding and depend entirely on large food masses, like *Lophogaster* (Manton, 1928, p. 110) and *Petalophthalmus* (Tattersall & Tattersall, 1951, p. 113). The number of thoracic limbs adapted to aid in feeding varies considerably. In the Lepidopidae, as in many Mysids, the first and second pairs are modified as maxilliped and gnathopod respectively. But others may also assist, though not specially modified—e.g. in many Mysidae all the thoracic endopodites may assist in dealing with large food masses, although this is not their main function (Tattersall & Tattersall, 1951, p. 30). In *Stygiomysis* the first four



FIGS. 29–32. *Hansenomysis fyllae* (Hansen). (Reg. no. 1909.xii.24. 100–103) Fig. 29. Labium and maxillula, in ventral aspect (paragnatha displaced by pressure of cover slip); above, paragnatha figured before mounting the preparation.

Indomysis annandalei Tattersall. (Reg. no. 1946.xi.26. 45–64). Fig. 30. Labrum, labium, left mandible and maxillula; below, right paragnath. (Preparation slightly flattened by cover slip). *Eucopia sculpticauda* Faxon. (Reg. no. 1949.vii.13. 65–75). Fig. 31. Right maxilliped, inner (or dorsal) surface. Fig. 32. Labium and left maxillula, in ventral aspect. (Scales for Figs. 29–32 all = 0.5 mm.). *b*. Sternal surface. *ex*. Exopodite. *l*. Paragnath. *p*. Mandibular palp. *u*. Upper lip or labrum. 4. Segment of endopodite distal to " knee ".

pairs are modified as maxilliped and gnathopods ; the same is true of the Eucopiidae, but here the following three pairs (5–7) are long and prehensile (see pp. 305 and 319). This brings up the question of the terminology of the thoracic appendages, which is discussed in the next section.

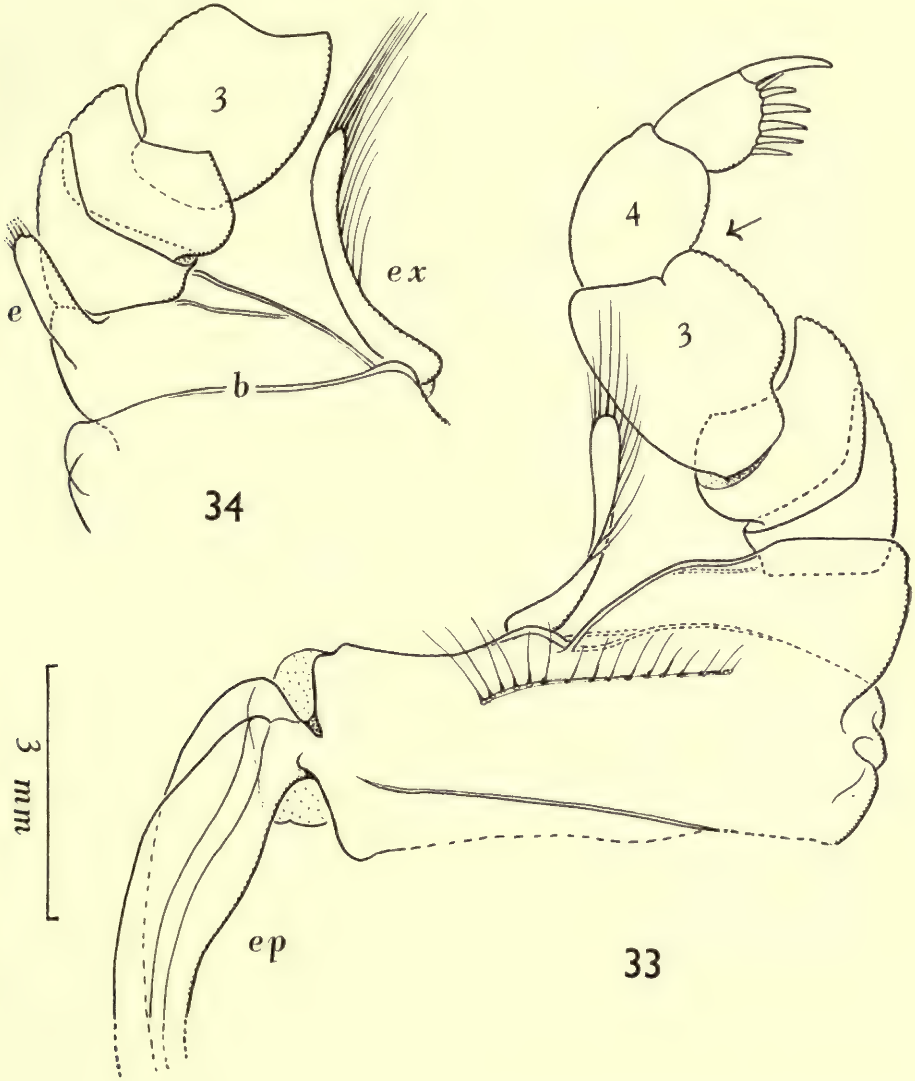
IV. TERMINOLOGY OF THE THORACIC APPENDAGES.

(*a*) TERMINOLOGY OF THE APPENDAGES. Various names have been given to the thoracic appendages of Malacostraca according to the special functions for which they may be adapted. Dr. O. S. Tattersall writes of the Mysidacea : " since different appendages may be adapted for this or that function in different genera, I consider such terms most confusing, and in this work I propose to use one term, thoracic limbs, for these eight appendages, and to refer to each under its appropriate number, irrespective of the particular function for which it has become adapted." (Tattersall & Tattersall, 1951, pp. 18–19.) That there is some confusion is apparent if one examines certain statements in the joint work just cited. For example, under the definition of the order Mysidacea (pp. 11–12) " first, and sometimes the second, pairs modified as gnathopods or maxillipeds " might be interpreted in different ways—that both pairs are either gnathopods or maxillipeds, or that one pair is to be regarded as maxillipeds the other as gnathopods. On p. 24 " *second thoracic limb* (= gnathopod or 2nd maxilliped) " is also ambiguous—are the terms used synonymously or not ? On p. 97 " endopods of the second to the fourth pairs of thoracic limbs . . . developed as gnathopods " implies that the first pair are maxillipeds. Most of the confusion centres round these two terms. Sometimes they are used synonymously ; sometimes each is used in a narrower sense, the anterior pair (or pairs) which are more markedly modified for " Nahrungszerkleinerung " being called maxillipeds in contrast to the less markedly modified succeeding pair (or pairs) of gnathopods (see Zimmer, 1927, pp. 302–303).

Nor is there agreement as to the number of pairs of thoracic appendages which are modified as maxillipeds in the various orders of Malacostraca (the term gnathopod is commonly used in literature dealing with the superorder Peracardia, rarely if at all in that dealing with Eucarida, Hoplocarida or Syncarida). In primitive types none of the thoracic limbs are differentiated as maxillipeds (Calman, 1909, p. 145) ; this is the case in Nebaliacea and Euphausiacea according to most authors. In other orders one, two, or three pairs are generally regarded as maxillipeds. With regard to the Stomatopoda Calman (1909, p. 322) wrote : " The first five pairs of thoracic appendages are similar in structure and are commonly called maxillipeds, though, as they possess no endites or other adaptations for mastication, the name is hardly appropriate ". Yet it is still often said that the Stomatopods have five pairs of maxillipeds—here the term gnathopod might be more appropriate. Hansen (1925, pp. 94, 128 and 154) thought that throughout the whole of the Malacostraca there is one pair of *real* maxillipeds. In his summing up (p. 154) he says : " *Maxillipeds and thoracic legs.*— . . . They are similar in Leptostraca, while in the other orders the first pair, the real maxillipeds, differ somewhat or considerably or very much from the following pairs, the legs." Yet even he inadvertently introduces further confusion because : (i) the reader has to bear in mind that his thoracic legs 1–7 are in reality thoracic appendages 2–8 and (ii) under the Decapoda he has reverted to the usual terminology of maxillipeds 1–3 and peraeopods or walking legs 1–5 (= thoracic limbs 4–8). Also under the Mysidacea he speaks of " intermediate " legs.

The terminology of the thoracic limbs has recently been discussed by Siewing (1958, pp. 250–251). The maxillipeds, he says, are chiefly adapted for chewing or filtering food and are characterized above all by the presence of endites. " Sind die Endite deutlich grösser als die den nach hinten folgenden Extremitäten, so wird man sie betreffenden Extremitäten als Maxillipeden von den folgenden differenzieren. In diesem Sinne ist das l Thorakalbeinpaar, zum Teil auch das zweite, der Mysidacea als Maxilliped zu bezeichnen, denn es besitzt an der Basis einen abgegliederten Endite ; Kaufortsätze werden ausserdem an Praeischium und Ischium beobachtet." Gnathopods, on the other hand, have he says their *distal* segments modified, often to form chelae or subchelae ; but according to Tattersall & Tattersall (1951, p. 24) the first thoracic limbs of Mysidacea may sometimes be subchelate.

Siewing's statement concerning the Mysidacea agrees in part with that of Calman (1909, p. 174) : " The first pair of thoracic limbs are always specialized as maxillipeds. In the Lophogastridae and Eucopiidae *they are without distinct endites* (italics mine). In the Mysidae an endite is generally borne on the basipodite, and sometimes also by each of the two following segments." Tattersall & Tattersall (1951, p. 97) also say that in *Eucopia* there are " no gnathobasic lobes on second, third or fourth segments ". If Siewing's definitions are strictly applied, the first thoracic limb of *Eucopia*, though smaller than, and appreciably different from, each of the three succeeding pairs of appendages, would also have to be called a gnathopod (see Text-fig. 31 of this paper). The same applies to the first thoracic limb of, e.g. *Mysidopsis* which also has no endites (gnathobasic lobes) on second, third or fourth segments (Tattersall & Tattersall 1951, p. 316) and to that of *Stygiomysis* although it is much smaller, and more intimately associated with the mouth parts, than are the three following pairs (Text-figs. 7, 9 and 10). Caroli (1937, pp. 22 and 226), who refers to the first pair as maxillipeds, gives the neatest possible definition of the next three pairs with his " Toracopodi 2–4 (gnatopodi) massillipediforme "! *Typhlolepidomysis*, on the other hand, exemplifies the two categories exceptionally well, having large endites on the first pair which are not pediform, none on the pediform second pair which have strong spines on the more distal segments. Unfortunately, Villalobos (1951, p. 205) refers to the latter as " primer par de pereiópodos " in the text and as " maxilipedo del secundo par " in the legend to Text-fig. 10. In *Lepidops* the second pair differs but slightly from the following pairs of thoracic limbs. In the family Petalophthalmidae the second thoracic limb has a large lamellar expansion on the ischium (merus of some writers) which, with its partner, forms a floor to the whole mouth region. (I have seen a specimen which had been preserved while enjoying a meal, and these lobes apparently help to retain the food mass while it is being chewed). Should this appendage be termed a maxilliped? It is much larger than the first thoracic limb (which in *Hansenomysis* has no endites) and its distal segments are modified to assist in manipulating the food mass. It seems illogical to term the first thoracic appendage a maxilliped in *Mysis* but not in *Mysidopsis*, in *Petalophthalmus* but not in *Hansenomysis*, in *Gnathophausia* (Text-figs. 33 and 34) but not in *Lophogaster*—see p. 316. Form depends on function and the feeding, locomotor and other habits of the animals determine how many appendages will be modified, and to what extent. The requirements of a raptorial animal differ



Figs. 33–34. *Gnathophausia ingens* (Dohrn). (Unregistered specimen from Madeira). Fig. 33. Right maxilliped, in ventral aspect. Fig. 34. Part of same, in dorsal aspect. *e*. Endite. *ep*. Epipodite. *ex*. Exopodite. 3 and 4. Segments of endopodite on either side of " knee " joint.

TABLE I.—*Segmentation of the Thoracic Endopodite in Eumalacostraca*

TERMINOLOGY of the endopodite—*i.e.* beyond basis. The claw is not a true segment.	A	B1	B2	B3	B4	C1	C2	D1	D2	E1	E2
	Calman 1909 and many authors	Hansen's (1925) terminology—adopted by Zimmer (1927) and by Tattersall and Tattersall (1951) in part.								Siewing (1958) in *Thermosbaena mirabilis*	
		Mysidacea Pl. vi, Figs. 2*a* and 2*b*.	Mysidacea Pl. vi, Figs. 3*a*, 4*a* and 6*a*	Mysidacea Pl. vi, Figs. 1*c*, 5*a*.	Mysidacea and other PERACARIDA Pl. vi, Figs. 10*e*, *f*.	EUCARIDA Pl. viii, Figs. 7*a*, 4*a*, 8*a*, 9*a*.	Pl. viii, Fig. 8*b*, 10*a*.	*Anaspides tasmaniae* Pl. v, Figs. 3*e* to 3*l*.		2nd thoracic limb.	3rd to 5th limbs.
basis	basis	basis	basis	basis	basis	basis		basis	basis + preischium	basis + ischium	basis
Segment 1	ischium	preischium	preischium	preischium	preischium	preischium + ischium	basis + preischium + ischium	preischium	ischium	merus	ischio-merus
										>	>
„ 2	merus	ischium	ischium	ischium	ischium	merus		ischium	merus	carpus	
	>					>			>		
„ 3	carpus or	merus	merus	merus	merus	carpus		merus	carpus	propodus	
	>	>	>	>	>			>			
„ 4	propodus	carpus	carpus	carpo-propodus (subdivided)	carpo-propodus (simple)	propodus		carpus	propodus	dactylus	
„ 5	dactylus	propodus (simple)	propodus (subdivided)	dactylus	dactylus	dactylus		propodus	dactylus	[strong claw]	
„ 6	[claw + or −] (often fused with dactylus)	dactylus	dactylus	[claw + or −]	[claw + or −]	[claw + or −]		dactylus	[claw]		
[7]		[claw + or −]	[claw + or −]					[claw]			

> = Position of " knee " joint.

from those of a filter feeder, even if the latter can also manipulate large food masses. The habitat to which an animal is adapted, even the niche within the habitat, may lead to modifications in both filtratory and raptatory feeders. *Eucopia*, with its long, slender " prehensile " endopodites 5–7, may remain suspended in mid water and seize any food that happens to come within range of these long legs, passing it on to the short gnathopods (2–4) ; it may even pursue its prey since the pleopods are well developed and natatory (see also p. 305). I fully agree with Siewing that terms ought to be properly defined, and that the terms under discussion need redefining. But, for the reasons given above, I do not think that one can apply his definitions too rigidly, within the order Mysidacea at any rate.

Cannon (1927) has shown that *all* the thoracic limbs in *Nebalia* are specially adapted for a unique mode of filter feeding. More recently Barkley (1940) has figured in great detail thoracic limbs 1–6 of *Euphausia* and has found that these six pairs together form an elaborate basket or filter for straining minute organisms from the water (the last two pairs of thoracic appendages are greatly reduced). In both these genera the similarity of the thoracic limbs would appear to be a secondary specialization rather than a primitive character.

(*b*) TERMINOLOGY OF THE SEGMENTS OF THE ENDOPODITE : There is also considerable diversity of opinion regarding the terminology of the segments in the endopodite of the thoracic appendages. In *Stygiomysis holthuisi*, for example, it is possible to interpret the parts numbered 1–6 in Text-figs. 9, 10 and 11 in three different ways : (i) ischium, merus, carpus, propodus, dactylus, and claw ; (ii) preischium, ischium, merus, carpus, propodus, and dactylus (with which the claw is incorporated); (iii) preischium, ischium, merus, carpo-propodus, dactylus, and claw. According to (i) the " knee " joint is at the junction of carpus and propodus ; according to (ii) and (iii) it lies between merus and carpus. This is why I have simply numbered the segments of the endopodite—those distal to the basis which bears the exopodite and is part of the protopodite.

The different terminologies which are in use are best shown in tabular form (Table I, which may not be complete). To the student reared on Calman's text book terminology **A** will be familiar ; according to this the " knee " joint is sometimes between merus and carpus, sometimes between carpus and propodus. The other terminologies (**B, C** and **D**) we owe to Hansen (1925). He maintains that there is an additional segment, the preischium, which is distinct in Peracarida but is often fused with the ischium (Eucarida) or with the basis (Syncarida). He also maintains that throughout the Eumalacostraca the " knee " is at the junction of merus and carpus and that, where there appears to be only two segments distal to the " knee ", the carpus is fused with the propodus (the claw is not a true segment and is not included). As shown in the table, this fusion of carpus and propodus occurs very frequently in Mysidacea and throughout the other Peracaridan orders. Siewing (1958) has recently studied *Thermosbaena* and his interpretation of the segmentation is shown as **E1** and **E2**. In minute animals like *Thermosbaena* and the Bathynellacea there is a reduction in the number of segments and it is by no means easy to decide where the " knee " is. Siewing thinks that here there is no preischium, and that the ischium is either fused with the basis or more or less completely fused with the merus.

In *Stygiomysis holthuisi* the number of segments in the endopodite is identical in each of the eight pairs of thoracic limbs (Text-figs. 7, 9–11). In each there are three segments proximal to the " knee " and three distal to it (including the claw or claw-like dactylus, according to the terminology used). Hansen would doubtless have regarded segment 4 as a fused carpo-propodus (**B**4) rather than as the carpus followed by the propodus and claw-like dactylus (**B**1). In Tattersall & Tattersall (1951, p. 24) it is stated that, in both first and second pairs of thoracic limbs of Mysidacea, carpus and propodus are always fused to form a single segment. Yet in fig. 42, C on p. 199 the first thoracic endopodite of *Erythrops elegans* (G. O. Sars) is represented as having *four* segments proximal to the " knee " joint and two plus claw distal to it. This can only be interpreted (if correct and not a slight lapse on the part of the artist) as : preischium, ischium, merus, carpus, [" knee "], propodus, dactylus and claw. According to Hansen the " knee " joint in Peracarida does not come at the junction of carpus and propodus. Since fig. 42, D shows the second endopodite of *Erythrops elegans* with only three segments proximal to the " knee ", fig. 42, C may not be correct. Hansen (1925) based his interpretation of the segmentation, in part at least, on a study of the muscles (see his figures of the distal segments of the thoracic endopodite in Mysidacea on pl. vi). In *Stygiomysis* there appear to be no muscle bands in segment 5, which might support Hansen's interpretation of 5 and 6 being dactylus and claw respectively. Perhaps the time has come for a thorough reappraisal of Hansen's work along the lines of the detailed functional analysis of limb structure undertaken in recent years by Dr. Manton in terrestrial Arthropoda (Manton, 1950–58—a series of papers on the Evolution of Arthropodan Locomotory Mechanisms ; the work is still in progress).

V. ADDITIONAL NOTE ON *SPELAEOGRIPHUS LEPIDOPS* GORDON

Order SPELAEOGRIPHACEA Gordon, 1957

Spelaeogriphacea Gordon, 1957, p. 45.
Spelaeogriphacea, Siewing, 1958, p. 267 ; Kaestner, 1959, p. 918.
" Reihe " Spelaeogriphacea Siewing, 1959, p. 110, Fig. 65.

Systematic Position. Siewing (1958, p. 247) placed the order Spelaeogriphacea among those Eumalacostraca with the telson and last abdominal somite fused. But, as stated in my original description and as shown in Pl. 4 of this paper, the sixth pleonite is free from, and much larger than, the telson. In a later work, which has just appeared, Siewing (1959, p. 110, fig. 65—cited in his 1958 paper as if it had already been published) has raised the Spelaeogriphacea to the rank of a "Reihe" or superorder, without apparently stating his reasons for doing so.

Since *Spelaeogriphus*, the only known genus, undoubtedly possesses a Peracaridan brood pouch composed of oostegites, I still regard the Spelaeogriphacea as an order belonging to the superorder (" Division " of Calman) Peracarida. Its precise relationship to the other Peracaridan orders cannot be determined until the internal anatomy and the embryology of *Spelaeogriphus* are known. However, from its external morphology, it appears to have affinities with the Tanaidacea, since it has a small but distinct carapace and a pair of cup-shaped respiratory organs beneath the carapace, near the bases of the first thoracic limbs (the maxillipeds). Siewing (1956, p. 87) has pointed out that in the Tanaidacea " der hinter dem Maxillipeden an der Körperwand liegende löffelartige Fortsatz ist kein Epipodit, wie Dohrn bei seinen embryologischen Untersuchungen zeigen konnte." (Dohrn, 1870, pl. xi). The respiratory organ in *Spelaeogriphus* may also be of this kind and not a true epipodite, but I called it an epipodite since that is the term commonly used in systematic descriptions of Tanaidacea.

However, I could not include *Spelaeogriphus* in the order Tanaidacea, since it differs in many respects from that group, having certain affinities with the Syncarida and with *Monodella* and some which are unique. In his earlier paper Siewing (1957, p. 267, phylogenetic diagram) placed it within the Peracarida, provisionally near the Isopoda-Tanaidacea line. Unless Dr. Siewing has studied material of *Spelaeogriphus lepidops* and has found that it differs markedly, anatomically and/or embryologically, from the other Peracaridan orders, his decision to separate Spelaeogriphacea from the " Reihe " Peracarida is premature, and in my opinion this step is unnecessary. It is a pity that this alteration was made in a text book because in all probability his phylogenetic scheme will be reproduced in future text books. The one thing that all Peracaridan orders have in common is that the young are incubated until a late stage of development in a *ventral* thoracic brood pouch or marsupium ; Siewing's (1958) separation of the order Thermosbaenacea from the true Peracarida is much more reasonable, since in both the known genera there is a *dorsal* carapacial marsupium. Stella (1959, p. 122) has accepted the " Reihe " Pancarida although she unfortunately refers to it as a " *phylum* ". Raising the Spelaeogriphacea to superordinal rank does not solve the problem of its relationships. The greatest caution should be exercised in establishing higher categories like superorders and subclasses until the animals have been thoroughly studied.

Genus ***SPELAEOGRIPHUS*** Gordon, 1957

Spelaeogriphus Gordon, 1957, p. 32.
Spelaeogriphus, Kaestner, 1959, p. 918.

Spelaeogriphus lepidops Gordon, 1957

Spelaeogriphus lepidops Gordon, 1957, p. 33, Text-figs. 1–26.
Spelaeogriphus lepidops, Kaestner, 1959, p. 918, Text-fig. 816.

ADDITIONAL MATERIAL. Bats Cave, Table Mountain, 30.ix.56, six specimens fixed in Bouin's solution (4 ♂, 1 ovigerous and 1 smaller ♀). From a stream at bottom of Bats Cave (temp. of water 50·5° F.), 1.ix.57, seven specimens (5 ♂, 1 ovigerous ♀ and 2 immature specimens).

REMARKS. The specimens were collected by the South African Spelaeological

Association; the 1957 material was fixed in 96 per cent ethyl alcohol (97 parts) and glacial acetic acid (3 parts). This fixative seems to be too drastic, causing the specimens to curl up to such an extent that in one instance the uropods got entangled among the thoracic appendages bunched up beneath the carapace region.

I have had several requests for a good figure of the entire animal, suitable for reproduction in a text book. My original Text-fig. 1 was incomplete, since I did not include the appendages, and Kaestner (1959, fig. 816) has based his figure on Dr. Barnard's sketch which I reproduced as Text-fig. 26 of my 1957 paper. The antennulae and antennae are not represented and these alter the look of an animal appreciably; in Kaestner's reproduction the first three thoracic exopodites look not unlike the gills of Lophogastrid Mysids. I take this opportunity, therefore, of publishing an original drawing of the whole animal, an ovigerous female, in dorso-lateral aspect as Pl. 4. This figure will also illustrate my article on Spelaeogriphacea which will appear in due course in the McGraw-Hill Encyclopedia of Science and Technology.

The female represented in Pl. 4 measures 6 mm. in length, from rostral apex to tip of telson, and the antenna is almost or quite as long as the body. The two antennular flagella are slightly unequal (they are more so in the male); the inner flagellum has about 30, the outer one about 24, segments. The faint line down the right side of the body, from carapace to first abdominal somite, is an artefact, a slight fold or crease in the integument. The marsupium contains ten to twelve rather large ova. I have not attempted to straighten out the thoracic limbs, which in preserved material tend to bend inwards beneath the body, because they easily break off if touched.

There is not much to add to my original description, since the animals do not seem to grow much larger; the largest male measures 8·6 mm. in length. Its antenna is at least 8 mm. long; the inner flagellum of the antennula is appreciably longer than the outer one and the number of segments in each is about 45 and 26 respectively.

In my original description I used Calman's terminology for the various segments of the thoracic limbs (see Table I, **A**). But, according to Hansen (1925), there is always a distinct preischium in the Peracarida (Table I, **B**1 to **B**4). The segments of the endopodite would thus be termed: preischium, ischium, merus, [" knee " joint], carpo-propodus and dactylus (Table I, **B**4). I have re-examined these appendages and in some there seems to be a faint indication of separation of the claw from the dactylus. In one specimen the distal sharp point is broken off neatly, beyond the longest spine on the ventral margin; this part doubtless represents the claw or nail (Gordon, 1957, Text-figs. 19 and 21–25).

The entire length of the gut is filled with a dark brown or blackish mass, suggesting that the animal feeds largely on detritus.

The registration numbers of the type specimens in the British Museum Collection are: holotype (♂), 1957.xi.12.1 and allotype (♀), 1957.xi.12.2.

I have a correction to make: in my 1957 paper (p. 43) I said that the Tanaidacea are entirely marine. But I overlooked a paper by Stephensen (1936) in which he described *Tanais stanfordi* from a freshwater lake in the Kurile Islands and mentions at least one other freshwater species from South America.

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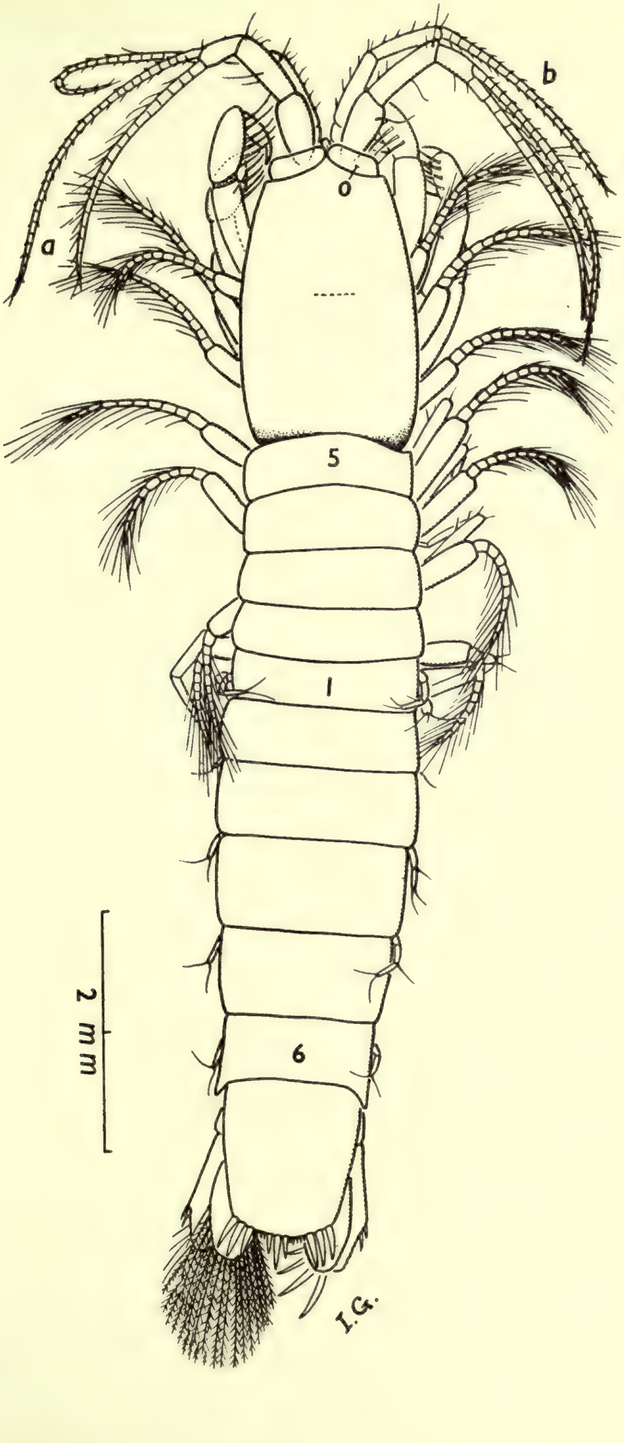
PLATE 3

Stygiomysis holthuisi (Gordon). Holotype, in dorsal aspect. *a.* Biramous antennula. *b.* Antenna. *o.* Ocular scale. 5. Fifth thoracic somite. 1 and 6. First and sixth abdominal somites.

PLATE 4

Spelaeogriphus lepidops Gordon. Ovigerous female in dorso-lateral aspect. *a.* Biramous antennula. *b.* Antennal flagellum. *g.* Respiratory exopodites or gills. *o.* Ocular scale. *s.* Antennal scale or exopodite. 5. Fifth thoracic somite. 1 and 6. First and sixth abdominal somites.

PLATE 3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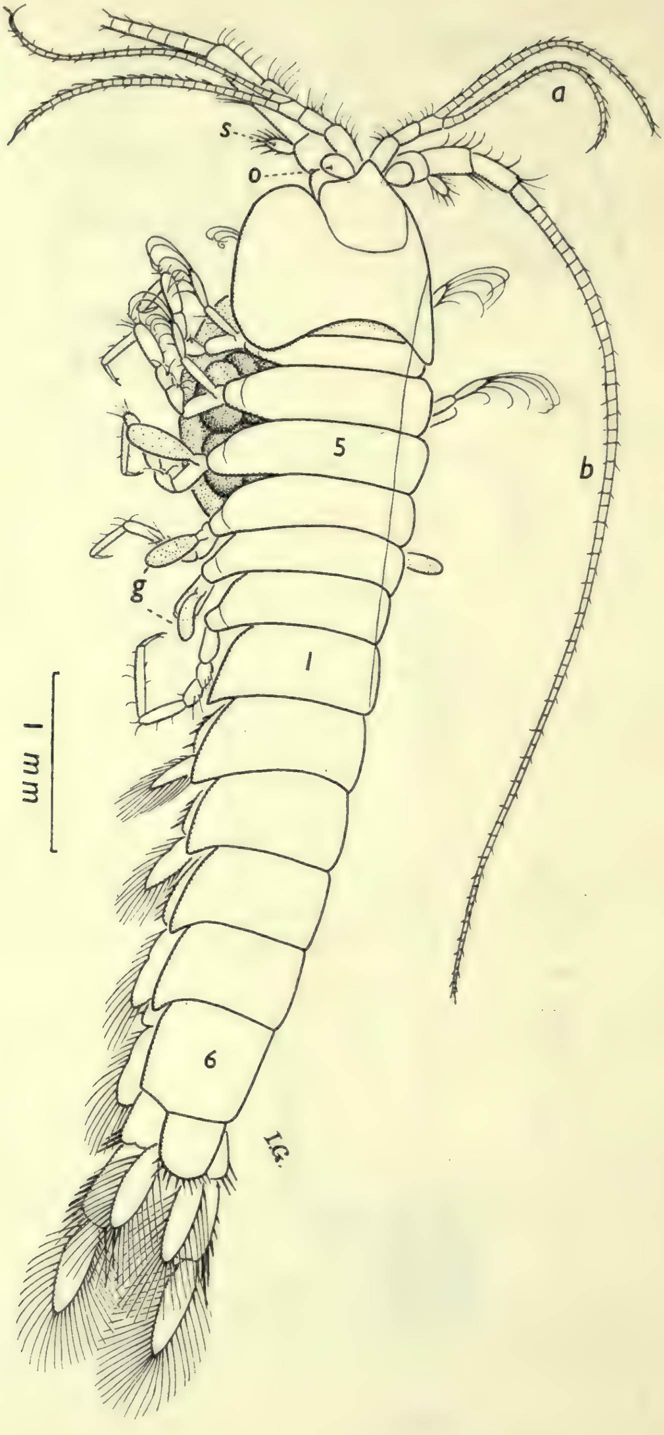
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CONTRIBUTIONS TOWARD A CLASSIFICATION OF MODERN ISOSPONDYLOUS FISHES

By WILLIAM A. GOSLINE

THAT the classification of the modern isospondylous fishes (Order Clupeiformes) is unsatisfactory would be admitted by all who have worked with them. The present contributions to the subject are divided into four sections. The first traces one structural complex, the caudal skeleton, through the whole group. The second and third have to do with controversial sections of isospondylous classification. In the final section a revised arrangement of modern forms, down to superfamily, is presented and its rationale discussed. The sections are in logical sequence, but it may also be noted that they are arranged in order of descending assurance on the part of the author. More, perhaps, than usual with classifications, that presented in section four is merely a " progress report ".

Regarding nomenclature, the ordinal, subordinal, and superfamily names are formed according to the system proposed by Berg (1940 : 353). The following procedures concerning common names have been adopted. Where an old literature name is well known it will be used. Thus the members of the order Clupeiformes will be called the isospondylous fishes, and those of the suborder Esocoidei the haplomous fishes. Where a common name in this paper ends in *oid*, it refers to a member of a suborder. For example, the term salmonoid fishes will be used to designate all of the forms of the Suborder Salmonoidei and not just those of the superfamily Salmonoidae. No common names will be used for superfamily[1].

Bone nomenclature is that of Devillers (1958).

The work on which this paper is based was nearly all done at the British Museum (Natural History) and I wish to thank the members of the fish division of that Museum for the facilities extended me and for permission to examine the skeleton and fish collection. I also wish to thank them, notably N. B. Marshall, for the discussion and suggestion of various points incorporated into the paper. The following individuals have been kind enough to read part or all of the manuscript and to offer constructive criticism : E. H. Ahlstrom, H. B. Bigelow, D. M. Cohen, D. H. Dunkle, N. B. Marshall, and G. W. Mead. Finally, I am greatly obligated to the John Simon Guggenheim Foundation for the fellowship that has made this work possible.

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[1] If Berg's termination *oidei* is used for suborder, the problem of devising different common names for subordinal and superfamily categories is equally great whether the superfamily ending *oidea*, recommended by the London Colloquium, or Berg's *oidae* is used.

SECTION 1. THE CAUDAL SKELETON OF MODERN ISOSPONDYLOUS FISHES

INTRODUCTION

The caudal skeleton of teleostean fishes has been the subject of papers by Barrington (1937), Blanco (1935), Hollister (1936, etc.), Kölliker (1860), Lotz (1864), Regan (1910*a* and *b*), Totton (1914), Whitehouse (1910*a* and *b*, 1918), and others. Nevertheless, the accumulated information is rather amorphous, and the caudal skeleton is usually either ignored or briefly dismissed in taxonomic papers. A large part of the difficulty would seem to stem from the failure to establish stable reference points as a basis for comparing one caudal skeleton with another : hence the introductory remarks that follow.

In a relatively simple caudal skeleton like that of *Amia* (Goodrich, 1909, fig. 311 or Whitehouse, 1910*a*, fig. 5), each of the last several vertebrae articulates with the base of a single caudal ray by means of a *hypural* (which is probably a hemal spine fused with the radial element of the fin ray, cf., Totton, 1914:255). In the teleostean fishes, however, complications of several types occur. In the first place, several of the posteriormost vertebral centra disappear (see below). Second, the hypural elements themselves become reduced in number, presumably through loss and fusion, so that in teleosts there are usually two to several caudal rays articulating with each hypural. Third, one or more elements of the caudal skeleton above the vertebral column lose their proximal contact with the neural arches (this is also true of *Amia*) becoming the so-called *epurals*. Finally, in the more primitive isospondylous fishes there are one to four pairs of bones that lie along the posterior end of the spinal cord ; these are the *uroneurals*.

A final term, *urostyle*, has been used in the literature to cover such a wide variety of structures that it will be completely avoided here. Supposedly the urostyle represents the last upturned vertebral centra. However, Regan (1910*a*) and Ramanujam (1929) have shown that the so-called urostyle of the Clupeidae is mostly formed of uroneurals (see footnote 2 of the present paper), and the uroneurals may form a large part of the " urostyle " of at least some higher teleosts.

Another difficulty lies in the fact that at least two of the centra at the end of the vertebral column in such a fish as *Elops* disappear as separate entities in the higher teleosts. Thus the last visible centrum of one fish is not always the homologue of the last centrum of another. To get around this difficulty it is necessary to establish some reference point that is both homologous and identifiable in as many teleosts as possible. The most satisfactory seems to be the posteriormost vertebra that is consistently present in all isospondylous fishes (except for such aberrant forms as *Coilia*) and is usually present in other teleosts ; this is here termed the *terminal vertebra* (TV of Text-figs. 1–15). It can usually be identified by a series of criteria (though the misimpression should not be given that any or all of these will easily or even securely establish the terminal vertebra of all fishes). The best single feature is probably the nature of the anteriormost hypural articulating or fused with it.

In most lower teleosts (and indeed in many percoids) the hypurals to the lower caudal lobe are quite constant in number (three) and general shape. The uppermost of these (HY3 of Text-figs.) is a rather narrow strut that is never expanded posteriorly. The next hypural below (HY2 of Text-figs.) is broadly wedge-shaped, i.e., considerably expanded toward the rear. Below this again is another strut-like hypural with a broad basal articulation or area of fusion with a centrum ; throughout the paper this will be considered the lowermost hypural (HY1 of Text-figs.), and the vertebra with which it articulates is the terminal vertebra. This hypural, or *hypural* 1, almost always differs from those behind and above it in having on each side near its base a lateral flange, which usually terminates posterolaterally in a sharp point. (This flange serves for the attachment of part of the flexor caudalis ventralis superficialis muscle (Greene and Greene, 1914 : 46) and probably in part as protection for the blood vessels that exit from the vertebral column behind the base of hypural 1. In these respects hypural 1 is the terminal structure retaining a number of hemal arch characteristics.) Generally, the terminal vertebra may also be identified in other ways. Whatever its relationship with centra (if present) behind it, there is always a normal, hourglass-shaped centrum and a typical intervertebral articulation immediately in front of it. More diagnostic perhaps is that if the front pair of uroneurals wedge into or fuse with any centrum, it is that of the terminal vertebra (except apparently in osteoglossoids).

In some recent teleosts one or two separately ossified centra may remain visible in the adult ; if so these are here termed *postterminal*[1] *centra* (PT of Text-figs. 1–4, 6, 7, 10 and 13–15) and are numbered from front to rear. When there are two postterminal centra, hypural 1 alone articulates or fuses with the terminal vertebra, and hypurals 2 and 3 arise together on the first postterminal centrum (as in Text-figs. 1–4).

Vertebrae just anterior to the terminal vertebra are here called *preterminal vertebrae* (PR of Text-figs.) and are numbered from back to front.

The structure of the upper half of the caudal skeleton seems to be more subject to variation than the lower. This is perhaps to be expected as there is phylogenetically a progressive retraction of the vertebral column from the upper caudal lobe. At any rate, in the isospondylous fishes there is some fluctuation, from specimen to specimen as well as from species to species, in the number of uroneurals and epurals, and from genus to genus in the number of upper hypurals.

Two other types of ontogenetic and individual variation should be mentioned. One is the abnormal but frequent doubling of the neural or hemal arches attached to any one centrum, even the terminal centrum (Totton, 1914 : 253). The other is the nature of the association between these arches and their centra. In young fishes the neural and hemal arches are wedged into their centra and only later in ontogeny do they fuse with them ; however, in some forms, e.g., *Albula*, such fusion never does take place.

Finally, it should be noted that dried skeletons, which have been used here, show especially the superficial features of the bones whereas stained and cleared specimens show more of the deeper features. Furthermore, for practical reasons dried skeletons are usually prepared from large adults whereas stained and cleared specimens are preferably small. Thus an investigation based on dried material is likely to emphasize one set of caudal features, that based on cleared specimens another.

---

[1] Dr. E. H. Ahlstrom informs me that he prefers to retain the term urostyle for those centra with which the hypurals articulate. If the confusion that has arisen from including the uroneurals in the " urostyle " can be cleared away, there is much to be said for this, especially in view of the term " postterminal centra " with its self-contradictory adjective that is used in this paper.

COMPARATIVE CAUDAL MORPHOLOGY

In the following accounts of individual caudal skeletons, a basal group (Diagram 1) is dealt with first. The " lineages " of caudal structure presumably arising from these basal forms are then discussed. Finally the component members of these " lineages " are taken up. Superfamily and subordinal names are those adopted in Section 4 of this paper ; for the moment it need only be noted that *Chanos, Kneria, Phractolaemus* and *Cromeria* are here included in the Gonorhynchoidei. Failure to mention certain families is due to lack of available material.

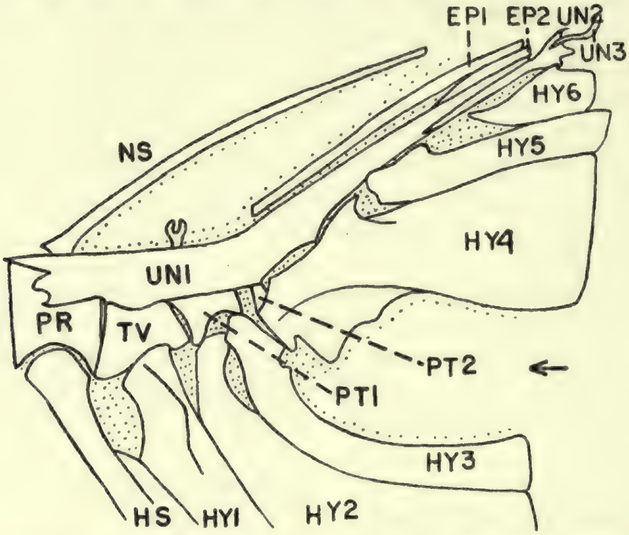
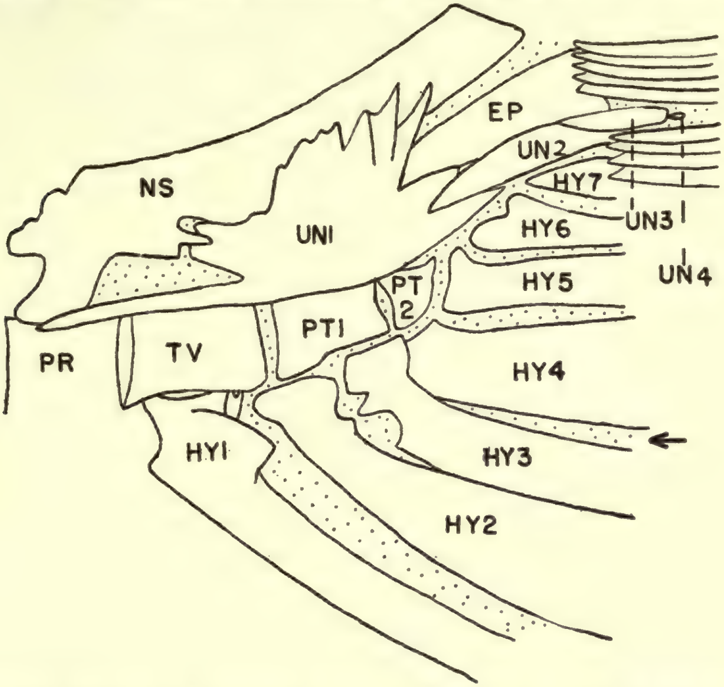


FIG. 1. Caudal skeleton of *Alepocephalus rostratus*, × $5\frac{1}{3}$. Stippling indicates interosseous or infraosseous areas. The arrow indicates the midpoint between the lobes of the caudal fin. EP, epural (these are numbered from top to bottom) ; HS, hemal arch and spine ; HY, hypural (hypurals are numbered from bottom to top ; hypural 1 is really in large part the hemal arch and spine of the terminal vertebra) ; NA, neural arch (only) ; NS, neural arch and spine ; PR, preterminal vertebra (these are numbered from rear to front) ; PT, postterminal centrum (theseare numbered from front to rear) ; TV, terminal vertebra ; and UN, uroneural (these are numbered from front to rear).

Of the caudal skeletons examined the following would seem to be among the most primitive[1]: *Elops* (Hollister, 1936, fig. 14), *Alepocephalus* (Text-fig. 1), *Salvelinus* (Text-fig. 2), *Esox* (Text-fig. 3), and *Hiodon* (Text-fig. 4). All of these have a number of unspecialized[1] features in common: the front end of the anterior uroneural overlaps, but neither wedges deeply into nor fuses with, the terminal vertebra; hypural 1 is the only hypural articulating or fusing with the terminal vertebra; hypurals 2 and 3, and these only, articulate with the first postterminal centrum; and a portion of a second postterminal centrum is always visible.

---

[1] Underlying the use of the terms " unspecialized " and " primitive " throughout this paper is the assumption that in teleostean fishes there has been a progressive fusion and loss of parts in the evolution of the caudal skeleton. (According to this concept the most highly simplified caudal skeletons are often the most " advanced " whereas the more complex are frequently the most " primitive ".)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HY1
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HY2

FIG. 2. Caudal skeleton of *Salvelinus grayi*, $\times 6\frac{2}{3}$. Bases of some of the upper fin rays are included to show gap for posterior uroneurals.

From the type of caudal skeleton represented in these primitive forms the more specialized caudal structures found among isospondylous fishes have presumably arisen. Indeed it seems possible to trace in the caudal skeleton four main " lineages " (I–IV of Diagram 1), as will be done here. As to these, *Elops* and *Alepocephalus*

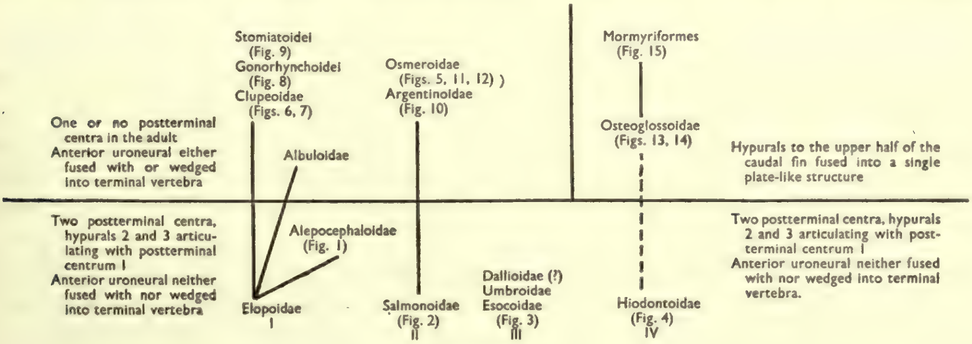
Stomiatoidei (Fig. 9)
Gonorhynchoidei (Fig. 8)
Clupeoidae (Figs. 6, 7)
Osmeroidae (Figs. 5, 11, 12))
Argentinoidae (Fig. 10)
Mormyriformes (Fig. 15)
Osteoglossoidae (Figs. 13, 14)
One or no postterminal centra in the adult
Anterior uroneural either fused with or wedged into terminal vertebra
Albuloidae
Hypurals to the upper half of the caudal fin fused into a single plate-like structure
Two postterminal centra, hypurals 2 and 3 articulating with postterminal centrum 1
Anterior uroneural neither fused with nor wedged into terminal vertebra
Alepocephaloidae (Fig. 1)
Two postterminal centra, hypurals 2 and 3 articulating with postterminal centrum 1
Anterior uroneural neither fused with nor wedged into terminal vertebra.
Dallioidae (?)
Umbroidae
Esocoidae (Fig. 3)
III
Elopoidae
I
Salmonoidae (Fig. 2)
II
Hiodontoidae (Fig. 4)
IV

Diagram 1

are considered to be basal members of a stock including the suborders Elopoidei, Clupeoidei, Gonorhynchoidei, and Stomiatoidei; *Salvelinus* represents the Salmonoidei; *Esox*, the Esocoidei; and *Hiodon*, the Osteoglossoidei and Mormyriformes.

Of these four presumed lineages, the caudal skeletons of adult members of the Salmonoidei (II) are, with the exception of those of the Salangidae and of the neotenic aplochitonid *Lovettia*, the most easily recognizable. In this suborder the last few preterminal vertebrae have neural and hemal spines with flattened, anteroposteriorly oriented blades (Text-fig. 5). These together tend to make up a flange or keel running above and below the posteriormost portion of the vertebral column. This structure is developed to a variable degree in the different salmonoid fishes but is only totally absent in *Lovettia* and the salangids; it is not found in the members of any of the other lineages, though *Albula* approaches it. In addition there is a series of about 10 small, more or less s-shaped accessory (procurrent) rays in front of the caudal fin above and below in the salmonoids including *Lovettia* and the salangids; these salmonoid accessory rays are easier to recognize than they are to differentiate from those that occur in many other isospondylous fishes.

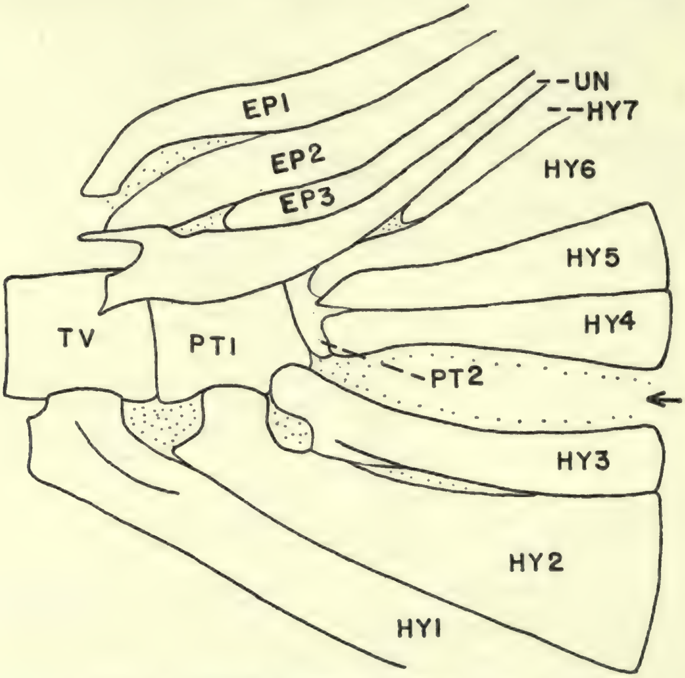

FIG. 3. Caudal skeleton of *Esox lucius*, × $2\frac{2}{3}$.

The osteoglossoid-mormyriform lineage (IV) has two quite different types of caudal skeleton, the one represented by *Hiodon* (Text-fig. 4) and the other by *Osteoglossum* (Text-fig. 13), *Heterotis* (Text-fig. 14), and *Mormyrus* (Text-fig. 15). It would be difficult to confuse the second type with any other isospondylous caudal skeleton, but it is quite possible that *Hiodon*, by a different route, may have produced a fish with a caudal skeleton similar to that in the clupeoid stock. The main caudal feature militating against a hiodontid derivation for such a fish as *Gonorhynchus* is that this genus and the great majority of the other fishes here assigned to Lineage I have 17 branched caudal rays, whereas all of the members of the osteoglossoid-mormyriform lineage including *Hiodon* have 16 or fewer branched caudal rays.

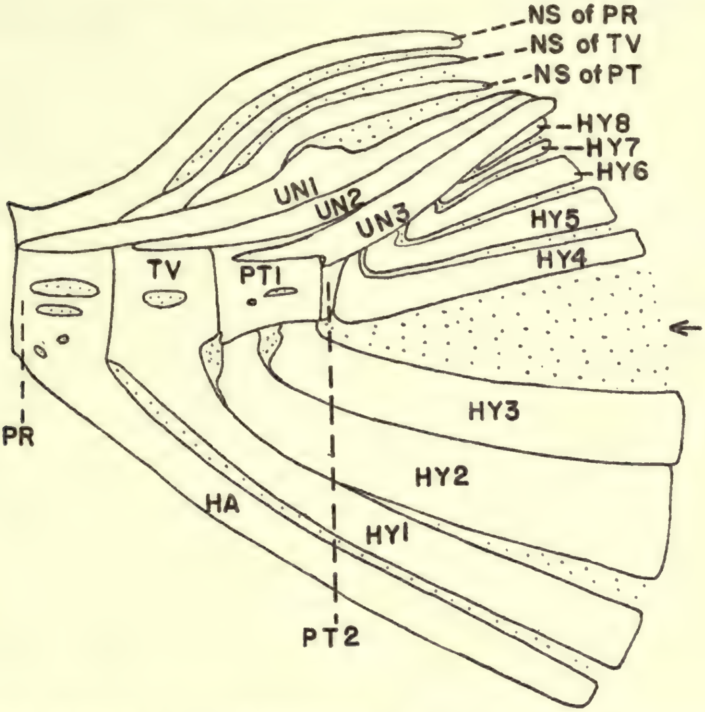

FIG. 4. Caudal skeleton of *Hiodon alosoides*, × $4\frac{2}{3}$. In this fish the preterminal and terminal vertebrae and the first postterminal centrum each have a neural arch and spine that articulates with its centrum between the lateral uroneurals of the two sides.

The haplomous lineage (III), as here understood, contains only the Esocidae, Dalliidae, and Umbridae. Chapman's (1944) assignment of the southern hemisphere aplochitonids, retropinnids, and galaxiids to the haplomous fishes is not accepted partly because of the caudal skeleton but also for other reasons that will be developed in Section 2 of this paper. The caudal skeletons of *Esox* (Text-fig. 3), *Umbra* and *Novumbra* are very similar and primitive. No caudal skeleton of *Dallia* has been available for investigation.

The final lineage recognized here is that including the clupeoids and various other groups (I). About the only feature held in common by all its members is the high number (17 except in *Coilia*, *Phractolaemus*, and *Cromeria*) of branched rays in the caudal. This would seem to distinguish them from the osteoglossoid stock.

The absence of antero-posteriorly directed flanges on the last few neural and hemal spines would in turn separate them from the salmonoids. Nevertheless, Lineage I as accepted here may prove to be a heterogeneous assemblage. For example, such groups as the Gonorhynchoidei and Stomiatoidei may very possibly have arrived at caudal skeletons similar to those of the Clupeoidae by a process of parallel or convergent evolution rather than because of genetic relationship: about all that can be said for these questionable groups is that their caudal skeletons do not seem to show relationships with the salmonoid, esocoid, or osteoglossoid lineages.

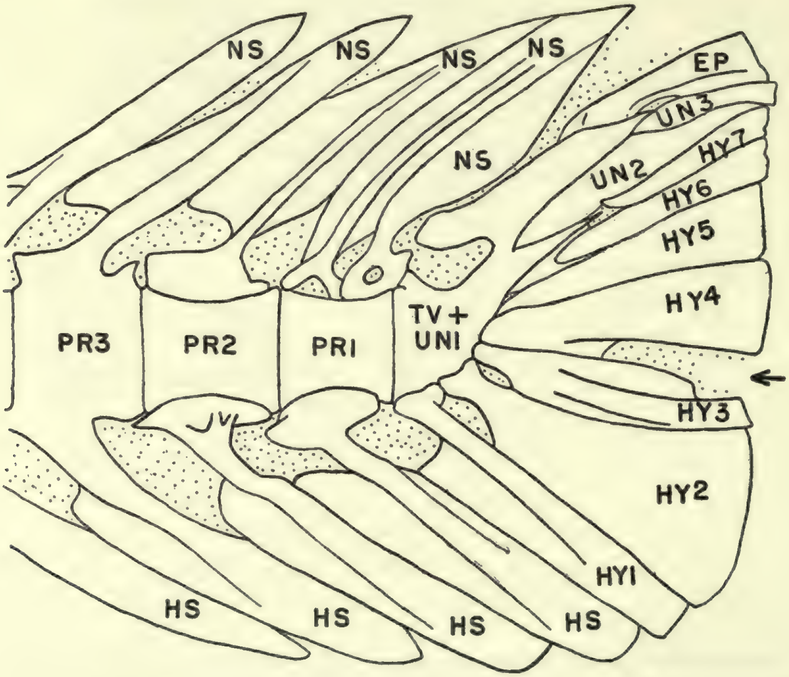

Fig. 5. Caudal skeleton of *Hypomesus olidus*, × 10$\frac{2}{3}$.

Suborder Elopoidei. Caudal skeletons of *Elops*, *Megalops*, *Albula* and *Pterothrissus* have been examined. All except the last have been discussed and figured by Hollister (1936, figs. 14–39). Though all are primitive, there is considerable difference between *Elops* and *Megalops* on the one hand and *Albula* and *Pterothrissus* on the other. In *Elops* and *Megalops* there are four pairs of uroneurals overlapping one another rather in the fashion of the body scales; in the adult *Albula* and in *Pterothrissus* there are only two pairs of uroneurals and these are arranged almost linearly, one pair behind the other. In *Elops* and *Megalops* the terminal vertebra bears a neural arch and behind it lies a small median crest above and between the uroneurals of each side; in *Albula* and *Pterothrissus* the terminal vertebra bears no neural arch and the median crest behind it has greatly expanded.

All of the species of Elopoidei appear to have 17 branched rays. *Elops* and *Albula*, but not *Pterothrissus* and *Megalops*, have a single bony fulcral plate at the front of the caudal base above and below.

Superfamily Alepocephaloidae. The caudal skeleton of *Alepocephalus* (Text-fig. 1) shows a peculiar combination of primitive (see above) and specialized features. There are the usual 17 branched caudal rays. Only one of the uroneurals is elongated, but this reaches forward to cover part of the first preterminal vertebra. Parts of two postterminal centra are visible, and hypurals 2 and 3 articulate with the first of these. Of specializations, the most notable perhaps is the long, curved, rod-like form of the upper epural and of the posterior neural spine.

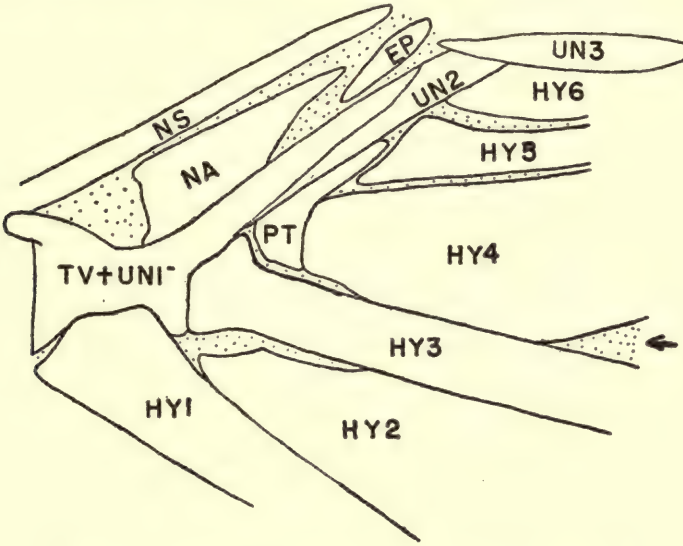

FIG. 6. Caudal skeleton of *Chirocentrus dorab*, × $4\frac{2}{3}$.

Superfamily Clupeoidae. The caudal skeleton of *Chirocentrus* illustrated here (Text-fig. 6) differs from that of the other clupeids and engraulids examined (aside from *Coilia*) only in the somewhat enlarged and long-based neural arch on the terminal vertebra and the very slight development of a lateral spine on hypural 1 (cf., Text-fig. 7). A specimen of *Nematolosa* examined, and illustrations of *Clupea* given by Ramanujam (1929, fig. 27) and of *Anchoviella, Harengula, Opisthonema,* and *Sardinella* by Hollister (1936, figs. 45–53) agree with *Chirocentrus* in all basic features. In these fishes the anterior uroneural is fused proximally with the terminal vertebra; hypural 2 has no basal articulation; one postterminal centrum is visible; and the neural arch of the terminal vertebra has a dorsally projecting flange that is usually higher than broad.

Many of these features have been developed in other isospondylous fishes but the loss of a basal articulation for hypural 2 apparently occurs only in portions of Lineage I. Normally, hypurals 2 and 3 articulate close together on a single centrum;

if two postterminal centra are present hypurals 2 and 3 articulate with the first, which would consequently indicate that when two postterminal centra are present the first is of double origin. In the herring, however, Ramanujam (1929) has shown by embryological investigation that it is the terminal centrum that is of double origin (it seems to be formed by the fusion of the terminal vertebra with the front half of the first postterminal centrum), and that presumably with this change hypural 2 has lost its basal attachment.

Though the anterior half of postterminal centrum 1 apparently always fuses into the terminal vertebra in the Clupeoidae, the fate of the more posterior centrum elements seems to vary. Thus, in *Clupea*, judging from Ramanujam's figures (1929, figs. 26, 27), the posterior half of postterminal centrum 1 fuses with the base of hypural 3; the same thing has probably occurred in *Chirocentrus* (Text-fig. 6) and the majority of Clupeoidae. In *Chirocentrus*, therefore, the element labelled PT is probably postterminal centrum 2, fused with such centrum elements as may occur behind it. From Hollister's figures (1936, figs. 40–45) it would appear that in the dussumieriid *Jenkinsiella* and perhaps in the engraulid *Anchoviella*, by contrast, the whole of postterminal centrum 1 fuses with the terminal vertebra. Finally, in *Dussumieria* it seems that the posterior half of postterminal centrum 1 has fused not only with the centrum elements behind it but with the base of hypural 3 as well. *Dussumieria* also differs from the other Clupeoidae examined in the fusion of hypural 1 with the terminal vertebra and the anterior uroneural.

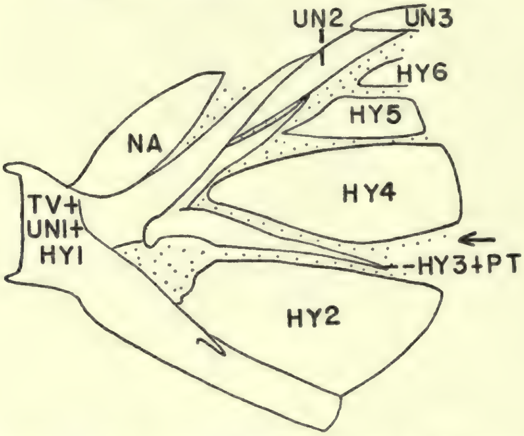

FIG. 7. Terminal vertebra and associated structures of *Dussumieria acuta*, × 7⅓.

Superfamilies Chanoidae, Phractolaemoidae, and *Knerioidae.* The caudal fin of *Chanos* differs in no very essential way from that of the herring-like fishes. The uroneural is completely fused at its base with the terminal vertebra, but the first hypural is merely suturally articulated. In the single large specimen examined neither hypural 2 nor 3 has any connection with a centrum. The one significant difference from the herrings would appear to be that the median projection between the basal wings of the uroneurals is low, and just above it, extending along the upper surface of the uroneural is a single long rod, presumably an epural. This structure is quite reminiscent of that in *Alepocephalus* (see Text-fig. 1) though little else about the caudal skeleton is similar.

The caudal skeletons of *Phractolaemus* and *Kneria* are in turn very similar to *Chanos*, differing from that of the herrings in approximately the same way as *Chanos* does. However, there are only 13 branched rays in the rounded caudal of *Phractolaemus*.

Superfamily Gonorhynchoidae. The caudal skeleton of *Gonorhynchus* (Text-fig. 8), as might be expected from the general consolidation of skeletal parts, shows a very high degree of fusion for the isospondylous fishes. Not only are the uroneurals ankylosed to one another and to the terminal vertebra along with hypural 1, but hypurals 2 and 3 appear to have fused with one another. In general appearance the caudal skeleton of *Gonorhynchus* bears considerable resemblance to that of *Dussumieria*, but whether this is a result of convergent evolution or of genetic relationship remains in doubt. In any event, the caudal skeleton of *Gonorhynchus* gives no indication of relationship with the Osteoglossoidae, and its 17 branched rays would militate against a possible derivation from *Hiodon*.

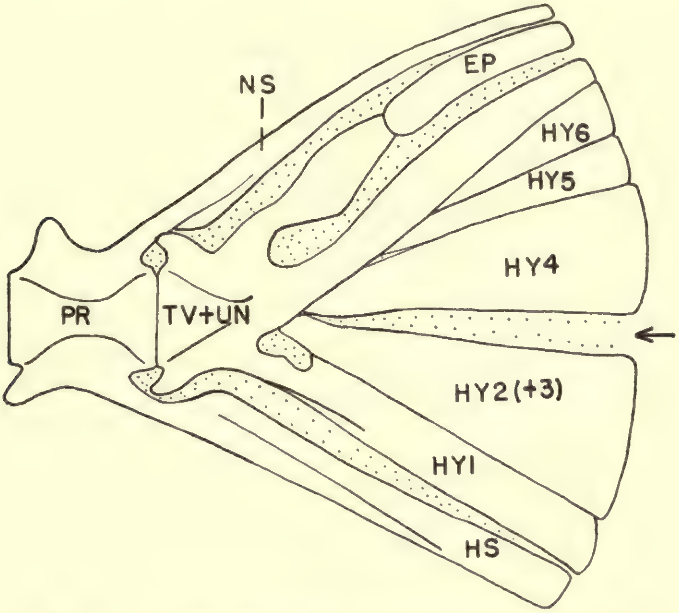

FIG. 8. Caudal skeleton of *Gonorhynchus greyi*, × 7⅓.

Suborder Stomiatoidei. Among the stomiatoid fishes the caudal skeletons of *Photichthys* (Text-fig. 9) and *Gonostoma* were the only ones available. These two differ considerably from one another. In *Photichthys* neither the anterior uroneural nor hypural 1 is fused with the terminal vertebra, but in *Gonostoma* both appear to be. In both genera there are the usual 17 branched caudal rays.

Superfamily Salmonoidae. The salmonids, thymallids, and coregonids (these terms are used here for groups of genera) all have a very characteristic and primitive caudal skeleton (Text-fig. 2). The anterior uroneural on either side bears a high crest between which the front ends of the epurals project. Two postterminal centra are visible ; hypurals 2 and 3 articulate with the first of these, but the base of hypural 2 also extends somewhat forward on to the terminal vertebra. *Salmo* and *Salvelinus* have a well-developed neural spine on the first preterminal vertebra (Text-fig. 2), but in two skeletons of *Thymallus* (see also Lotz, 1864, pl. 10) and one of *Coregonus* the epurals extend forward over but do not connect with the neural arch of the preterminal vertebra, thus replacing the neural spine in *Salmo*.

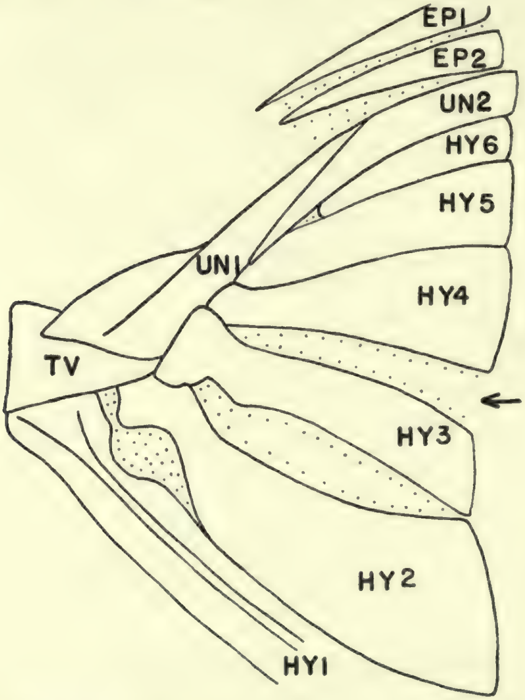

FIG. 9. Terminal vertebra and associated structures of *Photichthys argenteus*, × 7½.

Superfamily Argentinoidae. Among the Argentinoidae the only skeleton available is one of *Argentina*. This is here illustrated (Text-fig. 10) despite the strong possibility that the articulation between hypural 1 and the terminal vertebra is abnormal. Other available figures of the Argentinoidae are those of *Opisthoproctus* (Trewavas, 1933, pl. 2) and of *Macropinna* and *Nansenia* (Chapman, 1942*b*, fig. 6 and 1948, fig. 12 respectively). All of these show the typical salmonoid neural and hemal spine expansions. They may, however, be separated from members of the Salmonoidae by the fact that the anterior uroneural never extends forward of the terminal vertebra and from the Osmeroidae by the presence of at least one postterminal centrum.

Subsequent examination of two stained specimens, 38 and 46 mm. in standard length, of the bathylagid *Leuroglossus stilbius* (kindly loaned by D. M. Cohen), shows the same basic structure described above. However, the salmonoid flanges are entirely lacking on the smaller and only slightly developed on the larger example. As compared with *Argentina*, there are, in *Leuroglossus*, only two uroneurals, which are very slender, and the anterior of these is fused with the terminal vertebra. The postterminal centrum is considerably smaller than that of *Argentina* (Text-fig. 10), and only hypural 5 articulates with it. Also, *Leuroglossus* has no epurals.

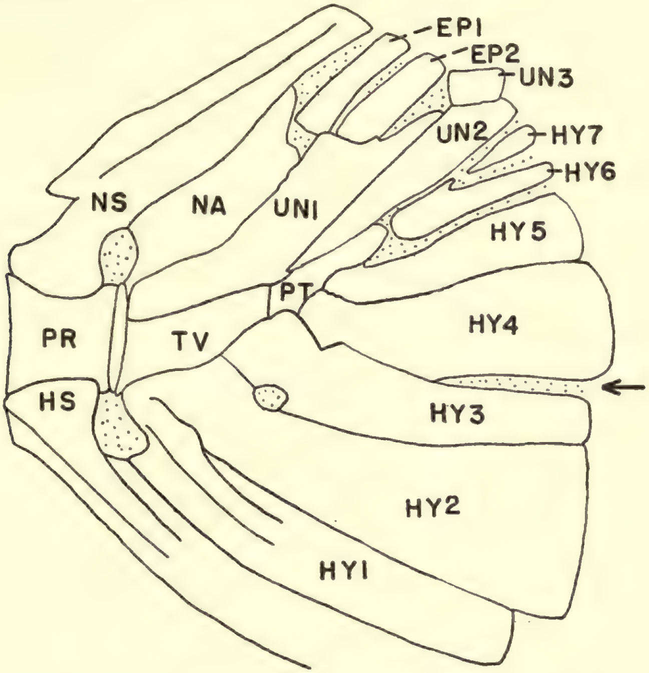

FIG. 10. Caudal skeleton of *Argentina silus*, × 6⅔.

Superfamily Osmeroidae. Of the members of the Osmeroidae mentioned below, all but the Salangidae and *Lovettia* have the typical salmonoid neural and hemal spines (Text-fig. 5). None of them show a postterminal centrum or for that matter any other caudal resemblance to the esocoids. Though there is considerable variation among the members the most striking skeletal difference is that in *Retropinna* and *Galaxias* (Text-fig. 11) the anterior uroneural is not fused with the terminal vertebra whereas in *Hypomesus* (Text-fig. 5), *Plecoglossus* (Text-fig. 12), *Aplochiton*, and the salangid *Leucosoma* it is. The caudal skeleton of the last-named genus is quite different from all of the others.

In one respect the caudal fins of the southern Osmeroidae differ from those of the northern members of the group (also from the Argentinoidae and Salmonoidae). All of the latter, including the salangids and *Plecoglossus*, have 17 branched caudal

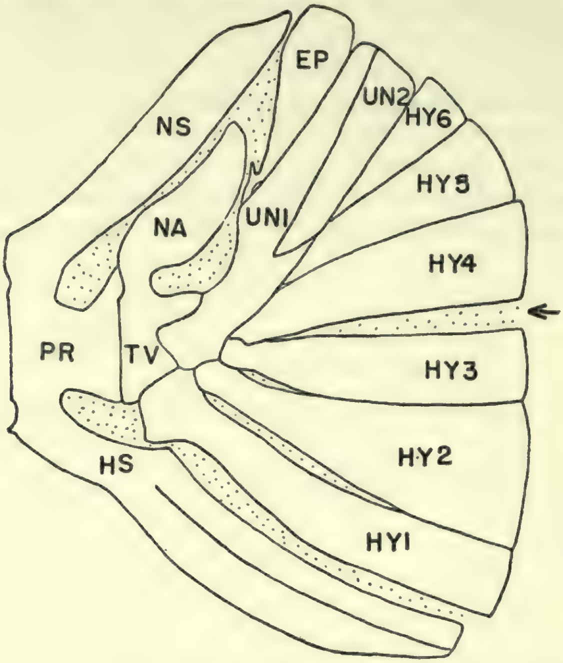
EP
UN2
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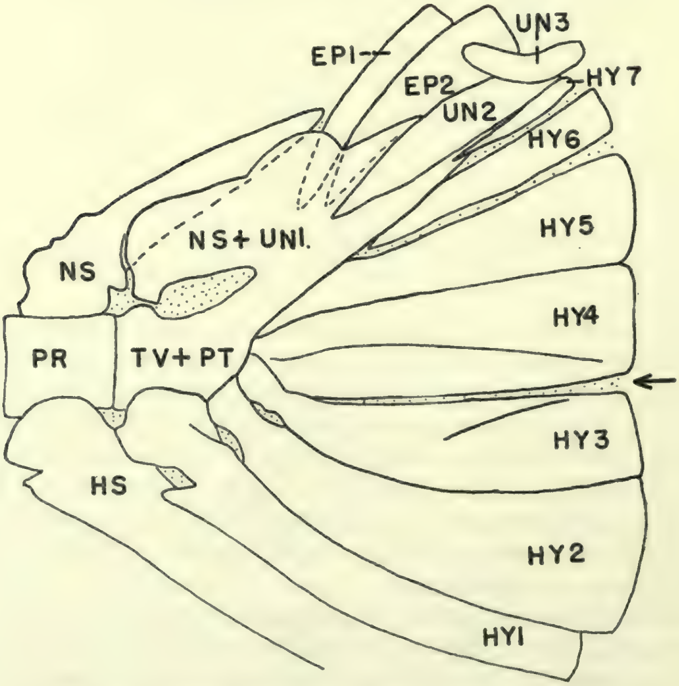
FIG. 11. Caudal skeleton of *Galaxias fasciatus*, × 6⅔.


UN3
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HYI

FIG. 12. Caudal skeleton of *Plecoglossus altivelis*, × 8.

rays. In the southern *Retropinna* and *Prototroctes* there are 16 branched caudal rays; and in *Aplochiton, Lovettia,* and *Galaxias* 14.

Suborder Esocoidei. The caudal skeletons of *Esox* (Text-fig. 3) and of *Umbra* are quite similar. That of *Umbra* appears the more primitive of the two, with six "hypurals" of about equal size between a narrower strut above and below. The upper of these struts is the uppermost hypural; the lowermost is the hemal arch from the second preterminal vertebra, the first preterminal vertebra giving rise to one of the broad "hypurals". In seven specimens of *Esox lucius* for which caudal rays were counted, five had 17 branched rays and two 16; for three specimens of *Umbra krameri,* two had 9 branched rays and one 8.

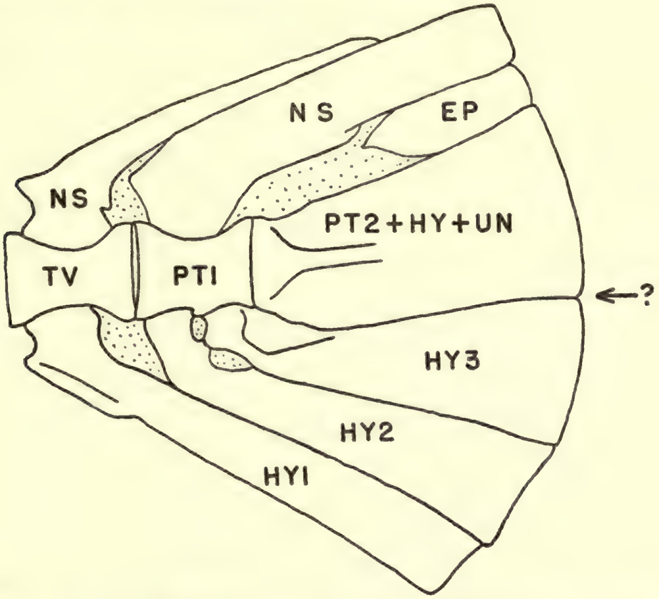

FIG. 13. Caudal skeleton of *Osteoglossum bicirrhosum,* × 5⅓.

Superfamily Hiodontoidae. As previously mentioned, one of the most primitive of isospondylous caudal skeletons is certainly that of *Hiodon.* In two skeletons examined, one of *H. tergisus* and one of *H. alosoides,* considerable variation appeared, not only from fish to fish, but on the two sides of the same fish. Thus the skeleton of *H. alosoides* has three uroneurals on one side (Text-fig. 4) and four on the other. In *H. tergisus* both the terminal and the first postterminal centra have double neural arches, and the anterior tip of the single epural runs in between but is free from the sides of the posteriormost arch. In *H. alosoides* (Text-fig. 4) both the terminal and the first postterminal vertebrae have single neural arches with spines that nearly reach the caudal fin base. Nine specimens of *H. alosoides* and one of *H. tergisus* examined all had 16 branched caudal rays.

Superfamilies Osteoglossoidae and Notopteroidae. The caudal skeletons of *Osteoglossum* (Text-fig. 13), *Pantodon,* and *Heterotis* (Text-fig. 14), while showing strong similarities to one another, are so different from those of all the foregoing isospondylous fishes as to be somewhat difficult to interpret. (*Notopterus*, see Whitehouse, 1910*b*, pl. 47, fig. 6 is even more specialized in the same direction, and a skeleton of *Arapaima* was not available.) Presumably, the terminal vertebra is that preceding the one to which two hypurals are attached. If this is correct, postterminal centrum 1 is present in an unusually complete form, and postterminal centrum 2 has fused with the large upper hypural plate and with the uroneurals as well (the latter fusion is incomplete in *Heterotis*, Text-fig. 14). Though any other interpretation of these caudal skeletons raises even more difficulties, the one just given presents three: first, hypural 3 in *Osteoglossum* has lateral flanges that are not found elsewhere in

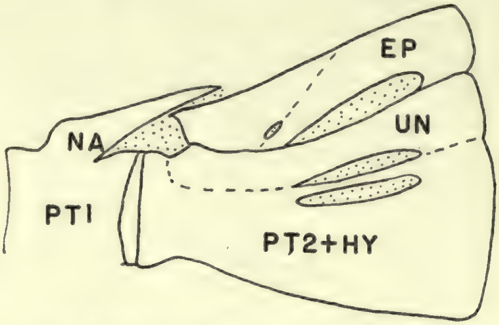

FIG. 14. Part of caudal skeleton of *Heterotis niloticus*, × 4⅔.

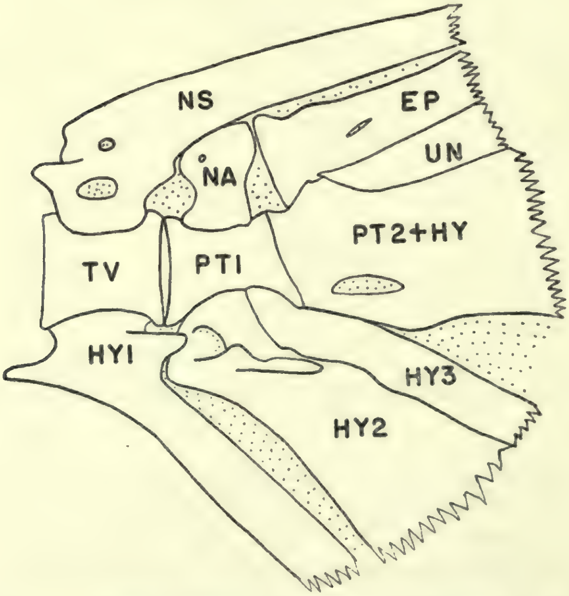

FIG. 15. Caudal skeleton of *Mormyrus caballus*, × 5⅓.

isospondylous fishes; second, postterminal centrum 1 in *Osteoglossum* has a neural spine instead of the usual epural structure; finally, and most oddly, the uroneurals in all three genera under consideration fuse with postterminal centrum 2 instead of with the terminal vertebra. Because of this last peculiarity, the alternate interpretation that what is here called postterminal centrum 2 is really the terminal vertebra deserves serious consideration. In any event, it is difficult to see how the caudal structure of these fishes has been derived from any of the isospondylous groups, including *Hiodon*, dealt with up to here. *Heterotis* has only 12 branched caudal rays, and *Osteoglossum* 14.

Order Mormyriformes. The caudal skeleton of *Mormyrus caballus* (Text-fig. 15) is basically very similar to those of *Heterotis* and *Osteoglossum*. The main differences lie in the flange on hypural 2 and the number of caudal rays in *Mormyrus* (16 branched).

DISCUSSION

Two subjects call for discussion. One is the functional significance of the different types of caudal skeletons noted above. The other concerns the bearing of the caudal structure on the limits of the order Clupeiformes.

Two aspects of the relation between structure and function will be considered[1]. The first of these concerns the elongate uroneurals of the primitive isospondylous fishes. According to Regan (1910*a*) and Ramanujam (1929) the uroneurals are, at least primarily, modified portions of neural arches of postterminal centra. Whatever their derivation, the elongation of these uroneurals in the so-called primitive isospondylous caudal skeleton is in itself a specialization. The only obvious explanation for these long uroneurals is that they stiffen the upturned terminal portion of the vertebral column. With the more abrupt upturning in this area found in advanced members of both the clupeoid and salmonoid lineages, the uroneurals, which start out as one or more shields along the sides of the postterminal centra, develop into struts which are at first wedged into the terminal vertebra and in more "advanced" forms fuse with it. Apparently a short, anchored strut serves here better than a long cover.

The second functional aspects has to do with the relationship between the caudal skeleton and the shape of the tail. In a very broad sense there is a correlation between these two features. Very generally, when the tail is forked the caudal skeleton is divided into distinct upper and lower portions, but when the tail is rounded the posterior outline of the hypurals is rounded, often with a number of hypurals of subequal size (e.g., *Amia*, *Umbra*) or with a central one somewhat larger than the others as in the cods. However, this relationship is far from strict. For example, the round-tailed serranid *Epinephelus* has the caudal skeleton of a typical fork-tailed fish. Conversely, the fork-tailed *Mormyrus* has a caudal skeleton that should belong to a round-tailed fish. Apparently the shape of the tail takes a very long time to imprint itself on the structure of the caudal skeleton.

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[1] In this discussion the caudal skeleton is treated as if it were an independent functional unit. Obviously it is not, for beside providing an axis for the basal articulation of the caudal rays it serves as a source of attachment for some of the caudal musculature (cf. Hindersson, 1910; Schmalhausen, especially 1913; and Greene and Greene, 1914) and for the transmission of the blood vessels and nerves to the caudal fin. However the role that these various functions have played in the evolution of the caudal skeleton are almost entirely unknown at the present time and have consequently been left out of consideration.

Similarly there seems to be a relationship, though again not a strict one, between the shape of the caudal fin and the number of caudal rays. In fork-tailed fishes the number is usually constant within groups. Indeed the basic number of 17 branched caudal rays runs through two of the four isospondylous lineages postulated here. However, a rounded caudal is often associated with a lower (and variable) number of principal caudal rays. Presumably, in a fork-tailed fish the greatest strength and functional importance lies in the outermost principal caudal rays which form rigid limits to the fin. In round-tailed fishes these outer rays lose their significance and the fin tapers from the middle to above and below. One is inclined to wonder whether those fork-tailed isospondylous fishes with some lower caudal count than the typical one, e.g., *Hiodon, Aplochiton,* have not had some round-tailed ancestors?

With regard to the information caudal structure can provide on the limits of the order Clupeiformes, there are only three groups that need be considered here : the haplomous, mormyriform, and iniomous fishes. Each of these has been included in or excluded from the Clupeiformes, depending on the classification adopted.

The first two of these groups have already been dealt with. Suffice it to say here that so far as the caudal skeleton is concerned the haplomous fishes appear to be as primitive as any of the isospondylous fishes. Since they stand at the base it is impossible to derive them from any other modern isospondylous fish, so far as the caudal skeleton is concerned.

The mormyroid caudal skeleton seems clearly to have been developed from the type now found in *Heterotis*. The structural inference, as already noted, is that the mormyrids retain not only the imprint established in a round-tailed form, but one of a peculiar and definitely identifiable type.

Among the iniomous fishes (Scopeliformes) only skeletons of *Neoscopelus, Lampanyctus, Aulopus,* and synodontid fishes have been available for examination. The caudal structure of these seems to be somewhat more primitive than that of many isospondylous fishes in that one postterminal centrum is clearly visible. In certain features, e.g., the flanged uroneural, these iniomous caudal skeletons appear to approach the salmonoid Clupeiformes ; however, they lack the expanded posterior neural and haemal spines of the salmonoids. In sum, there is little beyond an indication of possible relationships here.

Whether any or all of the three groups discussed above should be included in or excluded from the order Clupeiformes will, of course, depend in the first place on the nature of the whole animals, not just their tails, and in the second on a consensus of human opinion regarding what constitutes a fish order.

SECTION 2. THE CLASSIFICATION AND RELATIONSHIPS OF THE SALMONOID FISHES

The members of the Suborder Salmonoidei (as defined here) today are the dominant fishes in the coldest fresh water of both hemispheres. They are also represented in the temperate and arctic regions of northern seas by one group (Osmeridae) and in deeper oceanic waters by another (Argentinoidae[1]).

It is hardly surprising that there should be difficulty in defining as large and varied an assemblage as the salmonoids. Regan (1929) and others have differentiated them from the clupeoid groups by the absence or incompleteness of the oviducts. However, Kendall (1921) demonstrated that the oviducts of *Salmo* and *Osmerus* " are not radically different from those of other isospondylous fishes ". Regan (1913*a* : 289) gives the following additional salmonoid characters : an adipose fin usually present, one supramaxillary or none, and parietals well developed. Probably the most useful of these three features for purposes of differentiation is the adipose fin, for it is found elsewhere in the isospondylous fishes only among the stomiatoids and the Rosauridae. However, there are salmonoids (*Galaxias*) and salmonoid derivatives (the haplomous fishes) in which the dorsal fin has moved far back on the body and presumably squeezed out the adipose fin (Garstang, 1931 : 246–250). An adipose is also lacking in at least one of the oceanic salmonoids (*Microstoma*). An additional diagnostic trait of most salmonoids is that the last few " preterminal " vertebrae have laterally compressed neural and hemal arches, forming a flange above and below the posterior portion of the vertebral column (see previous section). This flange seems to be lacking only in the neotenic *Lovettia* and the Salangidae among the salmonoid skeletons examined. At least the posteriormost of these neural and hemal spines lead out to a series (usually about 10) of characteristic small, curved, accessory rays ; these occur prominently in both *Lovettia* and the salangids. A final trait that will apparently distinguish the salmonoids (and haplomous fishes) from the herrings and their relatives is the absence of a lower series of intermuscular bones, i.e., the series that articulates proximally with the base of the lower ribs (cf., Emelianov, 1935.)

The present classification of the salmonoid families stems from Regan (1913*a* : 289). There, he differentiates the families as follows :

" I. An orbitosphenoid ; an opisthotic ; a mesocoracoid ; vertebrae upturned at base of caudal fin . . . . 1. SALMONIDAE
II. An orbitosphenoid; no opisthotic; no upturned vertebrae; mesopterygoids toothless.
  A mesocoracoid ; parapophyses inferior . . . . . . 2. ARGENTINIDAE
  No mesocoracoid ; parapophyses lateral . . . . . 3. MICROSTOMIDAE
III. No orbitosphenoid ; no opisthotic ; no upturned vertebrae ; mesopterygoid toothed (absent in the Salangidae).
  A. A mesocoracoid ; maxillaries dentigerous, entering gape . . 4. OSMERIDAE
  B. No mesocoracoid ; maxillaries dentigerous, entering gape.
    Head compressed ; mesopterygoid well-developed dentigerous ; ribs ossified 5. RETROPINNATIDAE
    Head strongly depressed ; no mesopterygoid ; ribs not ossified . 6. SALANGIDAE
  C. No mesocoracoid ; maxillaries toothless, behind praemaxillaries.
    Praemaxillaries not extending whole length of maxillaries ; roof of myodome unossified ; no adipose fin. . . . . 7. GALAXIIDAE
    Praemaxillaries nearly reaching extremities of maxillaries ; roof of myodome ossified ; an adipose fin . . . . 8. HAPLOCHITONIDAE"

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[1] The name Argentinoidae, rather than Opisthoproctoidae, will be used throughout this paper for the perhaps over-simple reason that the most recent workers on the group (Hubbs, 1955 ; Bertelsen, 1958 ; and Cohen, 1958) seem to prefer the former name.

With regard to this classification, Regan goes on to say (op. cit.: 290) :

"It is of some interest to note that the Galaxiidae and Haplochitonidae are related to, but more specialized than, the Osmeridae, or Smelt family, of northern seas. *Retropinna*, from the coasts and rivers of Australia and New Zealand, is still nearer to the Galaxiidae and Haplochitonidae."

Subsequent work by Trewavas (1933), Parr (1937), and Chapman (1942*a*, 1942*b*, 1943, and 1948) has abundantly shown that the members of Regan's section II—including his Argentinidae and Microstomidae—are rather widely divergent from the other salmonoid fishes. Characteristic features of the group are the toothless upper jaw, the pelagic eggs, etc. The classification of the families within the group seems to be rather controversial (cf., the above papers, Hubbs, 1953, and Bertelsen, 1958) but the subject will not be entered upon here.

Similarly the members of Regan's (1913*a*) section I may be readily distinguished from all other members of the suborder by the three upturned caudal vertebrae. (Other members of the suborder have one or, at most, two.) Whether the family Salmonidae should be interpreted in the broad sense of Regan (1913*a*) or whether the Thymallidae and/or Coregonidae should be split off as separate families are matters that can best be left to those more familiar with these fishes to decide. However, the assignment of the fossil Thaumaturidae by Voigt (1934), Berg (1940) and others to the salmonid group seems to be open to some question. The typical salmonoid flanges formed by the last few neural and hemal spines are lacking, as is the adipose fin (acc. Voigt) ; the upward inflexion of the last three vertebrae shown in Voigt's pl. 2, fig. 5 is not salmon-like and is, in any event, not duplicated in the specimens shown in pl. 1, figs. 1 and 2 ; and the posterior position of the dorsal is more reminiscent of the haplomous fishes than of the salmons.

The last group of salmonoid fishes—section III of Regan—contains a rather diverse assemblage of fishes. It can, however, be immediately divided into a northern group of families—Osmeridae, Plecoglossidae, and Salangidae—with 17 branched caudal rays, and a southern hemisphere group—Retropinnidae, Aplochitonidae, and Galaxiidae—with fewer branched caudal rays. This subdivision is in line with Regan's (1913*a*) statements quoted earlier. Nevertheless both groups are quite varied within themselves, and each has given rise to a series of specializations partly paralleled within the other. Thus the northern *Plecoglossus* with its specialized dentition to some extent resembles the southern *Prototroctes* with its small flexible teeth, and the northern neotenic salangids are partly duplicated in the southern neotenic *Lovettia*.

The salmonoid allocation of the three southern hemisphere families remained uncontested until Chapman (1944), on the basis of an osteological study of *Aplochiton*, transferred the Aplochitonidae, Galaxiidae, " and very probably the Retropinnidae " to the haplomous fishes. Subsequent authors, e.g., Schultz and Stern (1948) and Wilimovsky (1951), have generally accepted Chapman's allocation. However, Blackburn (1950), from an investigation of the biology of the aplochitonid *Lovettia seali*, points out " that the life history of this species is similar to that of various salmonids, which makes the author incline to the views of Regan and Jordan " with regard to its systematic position.

In view of this difference of opinion, the British Museum material of the southern hemisphere forms has been examined. A general review of these, at least insofar as their systematic position is concerned, is undertaken in the following paragraphs.

In general the three southern families can be divided into two groups—the anadromous retropinnids and aplochitonids (*Prototroctes*?) with an adipose fin and a forked caudal, and the fresh-water or catadromous galaxiids without an adipose fin and with a rounded caudal.

The galaxiids would appear to be a fairly homogeneous group even though they are represented in southern South America, southern Africa, New Zealand, Tasmania, Australia, and presumably New Caledonia. Regan (1905) has an early revision of the family; more recently Scott (1936, etc.) and Stokell (1945, etc.) have worked on the systematics of the group. Swinnerton (1903) has written on the osteology of one of the species.

By contrast with the galaxiids, the retropinnids and aplochitonids are most diverse. The Retropinnidae has only a single Australian and New Zealand genus revised by Stokell (1941). The Aplochitonidae contains three very different genera: a fairly normal *Aplochiton* from southern South America and the Falkland Islands, *Proctotroctes* with a highly specialized dentition and with two almost if not entirely extinct species from Australia, Tasmania, and New Zealand, and the neotenic *Lovettia* from Tasmania. As already noted, Chapman (1944) has a paper on the osteology of *Aplochiton*, and Blackburn (1950) has published on the biology of *Lovettia*. A general account of the New Zealand forms of all three families is to be found in Stokell (1955).

In external characters, aside from those already mentioned, *Retropinna* and *Proctotroctes* are scaled; the other southern genera are naked. *Retropinna* has somewhat the look of, and is called, smelt (Stokell, 1955: 9–18, pls. 4 and 5) whereas *Prototroctes* looks rather like a *Coregonus* (Stokell, 1955: 41–44, pl. 13). *Aplochiton* is more trout-like (Eigenmann, 1927: pl. 15); *Lovettia* has a definitely larval appearance (Blackburn, 1950, pls. 1 and 2); and the galaxiids (Stokell, 1955: 19–40, pls. 6–12) have somewhat the look of the northern *Umbra*.

So far as I can see the rather variable fin counts have no significance for the classification of the group as a whole except for the caudal. Judging from counts in a single specimen of each genus, *Prototroctes* and *Retropinna* have 16 branched rays, whereas *Aplochiton, Lovettia* and *Galaxias* have 14 branched. All of these genera have the typical salmonoid accessory rays (see previous Section) at the front of the caudal above and below.

The dentition of these southern hemisphere forms is most varied. At the one extreme are certain species of *Retropinna* (Stokell, 1941) in which there is a long posterior portion of the maxillary, a short premaxillary, a crescent-shaped vomer, palatines, mesopterygoid, tongue, a long bone covering the basibranchials, pharyngeals, and dentary all with large teeth. At the other extreme is *Prototroctes* with fine, peculiarly-shaped, flexible teeth in the upper jaw and apparently none in the lower.

The maxillary is also variable. In the single genus *Retropinna* it may be toothed or toothless (Stokell, 1941: pl. 55). In the three genera of the family Aplochitonidae the toothless maxillary is excluded from the gape as effectually as it is in the perch-like fishes. A supramaxillary seems to be consistently absent.

In *Galaxias* and *Lovettia* the premaxillaries appear to be slightly protractile ; in both these genera they have rudimentary anterior pedicels.

With regard to the skull the parietals meet on the midline except in *Lovettia.* In a ripe female specimen of *Lovettia* both the frontals and parietals are elongate bones running along the superolateral borders of the skull. The whole median area of the skull roof is merely membranous, with the brain clearly visible.

The anterior ends of the frontals project well forward over the ethmoid, not only in *Lovettia* but in all the other southern genera as well. There are no proethmoids in any of them and what Chapman describes as proethmoids in *Aplochiton* (1944 : 150, fig. 1) are not separate elements in British Museum specimens but are merely anterior prongs of the frontals. (If these anterior portions somehow came to develop as separate elements in the northern haplomous fishes, would they not be proethmoids?)

Whether the mesethmoid is cartilaginous or bony in *Lovettia* is impossible to say ; it is certainly an endochondral formation. However, in *Galaxias* (cf., Swinnerton, 1903) there is a dermal mesethmoid as well.

I have not seen an orbitosphenoid in any of the southern hemisphere forms.

At the back of the skull the small supraoccipital is excluded from the foramen magnum in all the southern genera.

In the suspensorium the large mesopterygoid is usually toothed in southern forms. The metapterygoid extends forward over much but not all of the quadrate. There seems to be no knob behind the palatine for articulation with the lateral ethmoid (prefrontal). As to the ectopterygoid, it and the palatine seem to be fused into a single long, mostly toothed bone in *Retropinna.* However in *Prototroctes* the two elements are separate.

The suboperculum is a rather large bone forming part of the gill cover in all except *Lovettia.* In *Lovettia,* the suboperculum gives the distinct impression of being the seventh (and terminal) branchiostegal.

In the pectoral girdle, none of the southern forms has a mesocoracoid.

In the caudal skeleton there are never any visible " postterminal centra " (see previous section). The anterior uroneural may (*Galaxias*) or may not (*Prototroctes*) be fused with the " terminal vertebra ". In all, except *Lovettia,* the salmonoid flattening of the last few neural and hemal arches is distinctly developed.

As to soft anatomy, oviducts appear to be lacking in the females. In adult males of *Lovettia,* which seems to be unique in this respect, the urinogenital openings move forward to just behind the pectorals. None of the southern genera have pyloric caeca. *Lovettia* has a closed air bladder quite unlike that of the osmerids, salmonids, or northern haplomous fishes including salangids (N. B. Marshall, personal communication).

With this background regarding the southern hemisphere Aplochitonidae, Retropinnidae, and Galaxiidae, it remains to compare them with the northern hemisphere Esocoidei and Osmeroidae.

The northern haplomous fishes have been defined by Chapman (1934 : 372) as follows (and the definition has been accepted with little change by Berg, 1936, 1940, and 1955):

"Physostomous teleosts with the pelvic fins abdominal; cycloid scales; paired proethmoids; parietals separated by the supraoccipital; maxillary forming part of the edge of the upper jaw but lacking teeth; premaxillary not protractile; head scaly; the dorsal and anal fins far back on the body; but without adipose fin, mesocoracoid, or orbitosphenoid, and with no true spines in the fins."

As has already been noted, the southern hemisphere *Lovettia* has a closed air bladder; none of the southern forms have paired proethmoids; only *Lovettia* has the parietals in any degree separated by the supraoccipital; the maxillary is excluded from the gape in the Aplochitonidae, and in some species of the Retropinnidae the maxillary is toothed; in *Lovettia* and *Galaxias* the premaxillary appears to be slightly protractile; none of the southern forms have scales on the head; the dorsal in *Proctotroctes* is not especially far back; and only the galaxiids lack an adipose.

If, then, the southern hemisphere families are included in the Esocoidei, only the following portions of Chapman's (1934) definition are left intact:

"Teleosts with the pelvic fins abdominal; cycloid scales; anal fin far back on the body; without mesocoracoid or orbitosphenoid, and with no true spines in the fins."

The above words would apply, except for the absence of a mesocoracoid, to most Osmeroidae, and in toto to the included family Salangidae.

This is not to say that the southern families do not have haplomous resemblances, for they do. Indeed, some, but by no means all, of the similarities between *Aplochiton* and the haplomous fishes which Chapman lists (1944 : 164) will hold for all three southern families. Two more may be added here. First the southern families, like the northern Esocoidei, lack pyloric caeca, whereas the northern osmeroids (except the Salangidae) have several to very numerous caeca. Second, the southern forms all have fewer than 17 branched caudal rays, whereas the northern osmeroids all have 17 branched rays; in the northern haplomous fishes there is a reduction in caudal ray number except in *Esox*, and even here two of the seven specimens examined had fewer than 17 branched rays.

In comparing the southern families with the northern Osmeroidae, Chapman (1944 : 163) has already noted a number of differences, and several more may be added. The most important would seem to be the following: in the north a supramaxillary, mesocoracoid, epipleural ribs, and pyloric caeca are present (except in the Salangidae), whereas in the southern forms they are absent; and in the northern forms there are 17 branched caudal rays whereas there are 16 or fewer in the southern families. Admittedly these differences in the southern group are all modifications away from the basic salmonid type and in a haplomous direction. The same may be said of the posterior dorsal and anal position and the loss of an adipose in the galaxiids, which, of all the southern forms, have progressed farthest along this route. However, this direction has also been followed to a considerable extent by the northern salangids.

If, however, it is admitted that all three southern families are related and if the most primitive features of these families are added together, we have a fish that is basically osmerid. In *Prototroctes* the dorsal is median and the adipose is well developed. In some species of *Retropinna* the maxillary is toothed and indeed the whole dentition is osmerid, with the teeth of the tongue and basibranchials biting between those of the palatines and mesopterygoids. At the other end of the fish the salmonoid flanges on the neural and hemal spines are present (except in *Lovettia*) along with the curved accessory caudal rays, and the caudal supporting skeleton is osmerid (see Section 1).

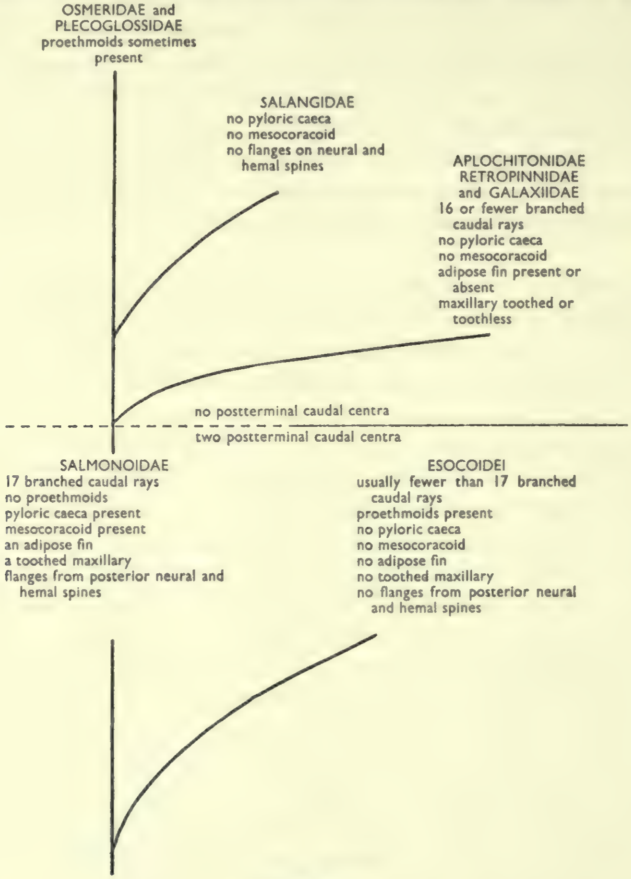
OSMERIDAE and PLECOGLOSSIDAE
proethmoids sometimes present
SALANGIDAE
no pyloric caeca
no mesocoracoid
no flanges on neural and hemal spines
APLOCHITONIDAE
RETROPINNIDAE
and GALAXIIDAE
16 or fewer branched caudal rays
no pyloric caeca
no mesocoracoid
adipose fin present or absent
maxillary toothed or toothless
no postterminal caudal centra
two postterminal caudal centra
SALMONOIDAE
17 branched caudal rays
no proethmoids
pyloric caeca present
mesocoracoid present
an adipose fin
a toothed maxillary
flanges from posterior neural and hemal spines
ESOCOIDEI
usually fewer than 17 branched caudal rays
proethmoids present
no pyloric caeca
no mesocoracoid
no adipose fin
no toothed maxillary
no flanges from posterior neural and hemal spines

Diagram 2

This last feature seems particularly important in view of the fact that the caudal skeleton of the haplomous fishes is not only very different but far more primitive than that of the northern and southern Osmeroidae. Finally, the anadromous life history of several of the southern forms recalls that of many salmonids. From all this it seems to the present author that the Aplochitonidae, Retropinnidae, and Galaxiidae are derivatives of a proto-osmerid stock that have evolved, some more and some less, in a haplomous direction; and that this same direction has been followed a third time to a lesser extent by the Salangidae (see accompanying diagram).

That the Salangidae and the southern hemisphere Osmeroidae have departed in the same direction from the northern Osmeroidae is indicated by the characters listed in the diagram. But the similarities between the salangids and the aplochitonid *Lovettia* are even more striking. Both *Lovettia* and the salangids are more or less neotenic, anadromous fishes, with tremendous sexual differentiation. The sexual differentiation, however, is of a very different type in the two groups : in the salangid males, but not the females, there is a series of large scales above the anal fin, and the fin itself has a peculiar curvature in several of the median rays ; in the adult male *Lovettia* the urinogenital papilla is just behind the pectoral fins. In the head of both, the posterior portion of the skull is very incompletely roofed by the frontals and parietals. Furthermore, these are the only two groups in the Salmonoidei that have no flanges on the preterminal neural and hemal spines.

In view of this it may appear that *Lovettia* and the salangids are closely related. Again I would prefer the hypothesis of parallel (neotenic) development. That *Lovettia* belongs with the southern osmeroids, and the salangids with the northern forms is indicated by the caudal ray count. In dentition, the salangids have a toothed maxillary typical of northern osmeroids, whereas *Lovettia* has a toothless maxillary excluded from the gape typical of the other two genera of aplochitonids. Additional characters for differentiating at least *Salangichthys microdon* from *Lovettia sealei* are the presence of a high (cartilaginous?) lump just behind the palatine for articulation with the lateral ethmoid (prefrontal) in *Salangichthys* and the absence of such a structure in *Lovettia* ; the presence of a well-developed subopercle in *Salangichthys* whereas the subopercle resembles a free branchiostegal in *Lovettia* ; the six branchiostegals of *Lovettia* vs. the four in *Salangichthys* ; and finally the normal, open salmonoid air bladder in *Salangichthys* vs. the peculiar closed one in *Lovettia* (see above).

A final question regards the interrelationships of the members of the southern group. Berg (1940) separated the galaxiids as a distinct order, primarily on the basis of brain structure. Unfortunately, all that is known about the brain of these southern forms seems to be a single remark by Swinnerton (1903) regarding *Galaxias*. However, there are other features that set *Galaxias* apart from the other southern osmeroids. Among these may be mentioned the general body form and the catadromous habits.

Another line of differentiation within the southern section of the Osmeroidae is shown by *Lovettia* with its neoteny, sexual differentiation, and closed swimbladder. Such peculiarities would certainly warrant family differentiation from the aplochitonids, except that the Aplochitonidae is already a family of only three genera. Furthermore, the two remaining genera—*Prototroctes* and *Aplochiton*—are also very different from one another, and it seems preferable not to erect three separate families each with a single genus.

Nevertheless, the fact remains that the southern Osmeroidae are now represented by several highly differentiated forms. Indeed, the differentiation is as great as in the northern Osmeroidae.

So far as the haplomous fishes are concerned, Berg stated in 1936 that the " Esocoidei are a specialized group of Clupeiformes originating from Osmeroid fishes at the end of the Cretaceous ". The present paper would tend, like that on *Aplochiton* by Chapman (1944), to demonstrate an even closer set of morphological links between osmeroids and esocoids than was known to Berg. However, the primitive caudal skeleton of the haplomous fishes indicates (see previous section) that *Esox*, *Umbra*, etc. have been derived from a somewhat less advanced salmonoid stock than the northern and southern Osmeroidae.

From the foregoing account, a classification (to superfamily) of the modern salmonoid fishes and their haplomous derivatives may be written as follows :

- Suborder Salmonoidei
  - Superfamily Salmonoidae
  - Superfamily Argentinoidae (= Opisthoproctoidae)
  - Superfamily Osmeroidae

- Suborder Esocoidei
  - Superfamily Dallioidae
  - Suprfamily Umbroidae
  - Superfamily Esocoidae

In this classification the three haplomous superfamilies of Chapman (1934) and Berg (1940, 1955) have been accepted without any attempt at critical evaluation. As to the salmonoid superfamilies listed here, everyone admits that they are related ; the only question is how to express the relationships. Here, the salmonid and osmerid groups have been recognized as separate superfamilies, and the argentinoids have been demoted to a superfamily equivalent to them. The first action is taken because it seems advisable, where feasible, to segregate a basal stock that has given rise to a number of lineages from the advanced members of those lineages.

The place that the Argentinoidae should hold in relation to the other two salmonoid superfamilies is somewhat less clear. Nevertheless it can only obscure the relationship that undoubtedly does occur to set the Argentinoidae up as a suborder (Opisthoproctoidei of Berg, 1940, Chapman, 1942*a*, etc.) with a taxonomic rank equivalent to that of the salmonoids themselves. In the specializations of the head skeleton (Chapman, 1942*a* and *b*), in the loss of a ventral mesentery (Kendall, 1935, Table I), and in the caudal skeleton (see previous section), the Argentinoidae is more specialized than the Salmonidae[1]. It would seem that the Argentinoidae is a much more divergent offshoot of the stock represented by *Salmo* today than is the Osmeroidae. But to express this greater divergence in a classification seems to lead to more incongruities than to consider them as a superfamily equivalent to the Salmonoidae and Osmeroidae.

SECTION 3. THE GONORHYNCHOID FISHES AND THEIR RELATIONSHIPS

The single modern genus generally attributed to the suborder Gonorhynchoidei is *Gonorhynchus* (cf., Regan, 1929 ; Berg, 1940 ; Wilimovsky, 1951 ; etc.). The systematic position of the suborder has always been dubious. Ridewood (1905*b*), on the basis of a study of the skull of *Gonorhynchus greyi*, while emphasizing its isolated position, tentatively suggests a distant relationship with the salmonids.

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[1] Another distinguishing character usually attributed to the argentinoids is the presence of a spiral valve in the intestine (cf., Kendall & Crawford, 1922). However, Cohen (1958 : 97, 98) has recently demonstrated that the " spiral valve " of argentinoids is not so diagnostic of that group as has usually been stated.

Regan (1929), in his synopsis of the isospondylous fishes, places the gonorhychids at the end of the order, behind the mormyrids. His basis for this placement is that the gonorhynchids have the " parapophyses ankylosed with centra, appearing as strong processes ". Subsequent authors, e.g., Berg (1940), Wilimovsky (1951), have generally accepted Regan's allocation.

That the parapophyses in *Gonorhynchus* are strong processes fused with the centra is true, but the value of this character in the classification of the isospondylous fishes seems dubious. For example, among the groups included by Regan in the section with *Gonorhynchus*, this genus and *Osteoglossum* have " strong processes " but *Hiodon* and *Mormyrus* appear to have none whatever, the ribs articulating directly with the centra.

A search for other characters that might indicate the relationships of *Gonorhynchus* discloses the following, all of which point toward an albulid-clupeid relationship. There are 17 branched caudal rays (this could equally well indicate a salmonoid ancestry). The caudal skeleton, except for the greater fusion of parts, resembles that of *Dussumieria*, the upright neural arch on the terminal vertebra being especially reminiscent of the clupeoids. Arising from the parapophyses are two sets of segmental bones ; one of these undoubtedly represents the lower ribs, but the other seems to be the lower intermuscular bones. Lower intermuscular bones again are characteristic of the clupeoids and seem to be absent from most, if not all, other isospondylous groups.

As to relationships within the great clupeoid stock, it is here suggested that the gonorhynchids belong with the chanids, phractolaemids, kneriids, and cromeriids. These five groups are so widely different that any relationship between them is difficult to comprehend. Yet the following similarities may be marshalled.

In external characters, the gill membranes are always attached to the isthmus, and in the three African families the gill openings are considerably restricted. In all, the mouth is small and toothless, or nearly so. The preopercular border is free only below (*Chanos*), if at all.

In the head the maxillaries run forward behind the premaxillaries and nearly or quite meet on the midline. There are no supramaxillaries. A preorbital bone extends forward above the upper jaw nearly to the end of the snout (this is least developed in *Chanos*). The preopercle extends only a short way up the side of the head and there may be a suprapreopercular (*Phractolaemus* and *Chanos*) or a long tube-containing ossicle (*Kneria*) above it. The lower preopercular limb, however, runs well forward and forms the chief support for the quadrate. On the skull roof the frontals are large and the parietals are very small and almost restricted to the rear border of the skull, with the supraoccipital separating those of the two sides. The supratemporal commissure of the lateral line either runs across the parietals and supraoccipital through a series of superficial ossicles or through these bones themselves.

In *Gonorhynchus* and *Chanos* the exoccipitals send out a pair of prongs that roof the anterior portion of the spinal cord ; in the flat-headed *Kneria* and *Phractolaemus* the projection of the supraoccipital serves the same purpose, with the walls of the first few neural arches forming the sides.

The lower intermuscular bones are present in *Chanos* and *Gonorhynchus*, apparently absent in *Phractolaemus* and *Kneria*. In *Gonorhynchus* the lower ribs are short and slight, and articulate with lateral expansions of the centra. In *Chanos* the ribs are large and their upper portions articulate directly with the centra, the lower by way of a bony nodule. In *Phractolaemus* and *Kneria* the ribs articulate directly with the centra but in the former the ribs are very strong, in the latter moderate. Admittedly, these vertebral characters show little relationship between the genera, but they are given because of their previous use in classification.

The caudal skeleton of all these groups (*Cromeria*?) is essentially the same.

As to mode of life, *Gonorhynchus* is today a purely marine fish, but the group to which it belongs is known from Eocene fresh-water deposits from America and Europe. *Chanos* is euryhaline, and the other three genera are restricted to fresh water. All five genera are tropical.

A good many of the similarities in these five groups may be primarily or secondarily related to the small size of the mouth in all these forms. It could therefore be that the small mouth has developed independently two or more times and that all of the other changes have followed as a matter of course. Some check on this possibility is offered by the members of the Argentinoidae, a small-mouthed group in the salmonoid stock. To some extent a parallel evolution is indicated between the Argentinoidae and the five groups taken up here, particularly with regard to jaw structure, suspensorium and the reduction in branchiostegal rays. However, there are a number of features in the five groups that are not duplicated in the Argentinoidae. Among these are the attachment of the gill covers to the isthmus, the loss of the normal upper portion of the preoperculum, the passage of the supratemporal commissure over or through the supraoccipital, the expansion of the anterior portion of the spinal canal, and the advanced form of the caudal skeleton.

To summarize, the argument presented here is not that *Gonorhynchus*, *Chanos*, *Cromeria*, *Kneria*, and *Phractolaemus* are closely related. Indeed, no two of them are. It merely seems to the author that each of the five is more closely related to the others than it is to anything else. If this is granted, then it becomes fairly easy to tie in the group, via *Chanos* and to some extent *Gonorhynchus*, with the general clupeoid stock[1].

SECTION 4. A CLASSIFICATION OF THE MODERN ISOSPONDYLOUS FISHES

The systematics of the living isospondylous fishes have received a great deal of attention. Because of the excellent literature review by Wilimovsky (1951) only a sampling of papers on the subject need be mentioned here.

With regard to the general classification of the groups of Clupeiformes the deservedly classical papers are those of Ridewood (1904*a* and *b*, 1905*a*, *b*, and *c*). Unfortunately Ridewood studied only the head skeletons of a limited number of isospondylous groups. Regan (1913*a*) dealt briefly with the classification of the salmonoid fishes and in 1929 presented a synopsis of the full order. Berg's (1940) volume introduced some rather drastic innovations. Chapman (1934–1948) has written a number of valuable papers on the relationships of individual members of the group, and Norman (1957) gave a key to the suborders, families, and genera.

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[1] The British Museum (Natural History) material upon which the above account has been based consists of complete skeletons of *Gonorhynchus* and *Chanos*, somewhat incomplete skeletons of *Practolaemus* and *Kneria*, and a stained and partially cleared skeleton of *Kneria*. Whole specimens of all genera mentioned have been examined. For the osteology of *Cromeria*, reliance has had to be placed on the paper by Swinnerton (1903). Ridewood's accounts of the head skeletons of *Phractolaemus* (1905*a*) and *Gonorhynchus* (1905*b*) have also been used.

Besides the above and many other papers dealing more or less directly with isospondylous classification, a large number of works bear indirectly on the subject. For example, Ford (1937) took up variations in the vertebral column. Whitehouse (1910*a* and *b*), Regan (1910*a* and *b*), Hollister (1936, 1940), and Schaeffer (1949 : 13, 14) have taken up the caudal skeleton. Starks (1930) wrote the most complete account of the pectoral girdle. Frost (1925) took up isospondylous otoliths. Allis (1904), Wohlfahrt (1937), and Nybelin (1957) have dealt with the lateral line system of the head. Van Dobben (1935), Hofer (1945), Tchernavin (1953), Günther and Deckert (1953, etc.) and Kirkhoff (1958) have taken up various aspects of the functional morphology of the head. As to soft anatomy, Bridge (1900), de Beaufort (1909), Svetovidov (1950, etc.), Jones and Marshall (1952), and O'Connell (1955) investigated the air bladder. Boas (1880) and Senior (1907, etc.) reported on the heart. Jacobshagen (1912) and Suyehiro (1942) have made comparative studies of the digestive system . Finally, Hyrtl (1856), Lagler and Kraatz (1945), Kapoor (1954), and Takahashi (1957) have dealt with the epibranchial organ.

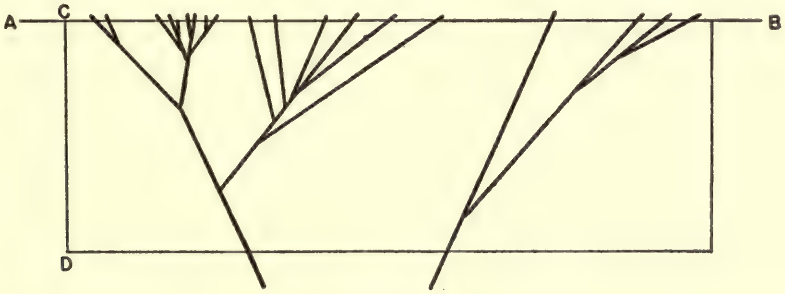

Diagram 3

Despite all of the work that has been done, the classification of the isospondylous fishes (Order Clupeiformes) remains unsatisfactory. Indeed, Berg (1940 : 417) has written : " This order, from which a series of higher orders has arisen, represents an artificial assemblage, its separate members, as may be seen from the diagnosis, differing greatly from one another. In time the Clupeiformes will be, doubtlessly, divided in many orders ". Berg's view, I think, stems at least in part from a tendency to look at isospondylous classification at a single time level, for example AB of Diagram 3, whereas if a time dimension, CD, were incorporated into the concept, the " artifical assemblage " aspect would seem to largely disappear. In any event there are four main questions that need to be answered with regard to isospondylous classification. (1) What are the interrelationships of the living members? (2) What are the relationships between living and fossil members? (3) What are the limits of the group? (4) How can it be defined?

Here, no effort will be made to deal with fossil forms. The classification of fossil Clupeiformes is a large and important subject in itself, and one to which the present author can make little contribution as he has no first hand familiarity with fossil material.

The classification of modern isospondylous fishes that follows thus attempts to reconstruct phylogenetic relationships from a knowledge of fishes at only one time level and is consequently prone to all the pitfalls inherent in such a procedure. Yet there are certain points to be made in justification of such a classification. One is that it provides a corpus for the paleontologists to work from, with, or even against. More important, however, is the fact that ichthyologists working with modern fishes are obligated to do as much as they can with the fishes around them. There is virtually no chance that neotenic fishes like *Cromeria* and *Lovettia* will ever turn up in the fossil record. Indeed one is inclined to wonder whether the fossil record would not give a very peculiar picture of isospondylous classification because of the overrepresentation of some groups and the underrepresentation of others. Thus the salmonids are usually stream dwellers and are unlikely candidates for fossilization ; the same might be said of the oceanic stomiatoids. Again, some of the most peculiar of the isospondylous fishes are from African fresh waters, and pre-Pliocene fish remains from that continent are as yet few. On the other hand certain of the isospondylous fishes, notably the herring-like forms, seem frequently to die in areas where they fossilize in relative abundance. Thus if the major groups of the paleontologist, e.g., the chirocentrids, do not always correspond to the major groups of the modern ichthyologist, that may merely mean a difference in viewpoint rather than an error in interpretation. Eventually, of course, a single classification of isospondylous fishes based on both fossil and recent material will have to be developed, but the time to attempt this hardly seems to have arrived.

As to a hard and fast definition of the Clupeiformes, that, as might be expected of any group so diverse, is impossible except in negative terms. Apparently about the best that can be done is as follows :

Caudal fin homocercal. No true spines in the fins. Pelvic fins abdominal and with more than 5 rays (although in the Notopteridae the pelvics are absent or rudimentary and few-rayed, and the Notopteridae, *Pantodon* and *Macristium* have subthoracic pelvics). Maxillary usually included in the gape. Scales, if present, cycloid (except *Gonorhynchus* and certain species of argentinids and osmerids). Air bladder, if present, physostomous (except *Lovettia*, stomiatoids, and Argentinoidae). Orbitosphenoid and mesocoracoid generally present ; branched caudal rays most frequently 17. No Weberian ossicles. Lateral line, if present, not running low on sides. Snout not tubular. No electric organs.

With regard to the limits of the Clupeiformes, both the " upper " and the " lower " borders of the order have been the subject of controversy. Thus Saint-Seine (1949) removed *Elops* from the isospondylous fishes and placed it in the Halecostomi, and Nybelin (1957) has stated that *Elops* is as much a holostean as *Amia* or *Lepisosteus*. Here, *Elops* will be retained in the Clupeiformes, with the full realization that it becomes extremely difficult to place a lower limit on the order when fossil material is taken into account.

At the " upper " limit there are six groups of fishes that have been at times included in and at other times excluded from the Clupeiformes by modern authors. That the Anotopteridae, included " incertae sedis " by Berg (1940 : 435), belongs among the iniomous fishes has been adequately shown by Maul (1946) and Nybelin (1946). Berg (1940 : 436) creates a separate order for the Galaxiidae, but this family may apparently be returned to its usual place in the Clupeiformes (see Section 2). The Bathyclupeidae has been juggled about by various authors, sometimes landing in the isospondylous fishes, but it belongs with the percoids where Regan (1913*b*) placed it (N. B. Marshall). The three remaining groups are more controversial. The gymnarchid-mormyrid stock can be traced back with considerable certainty into the osteoglossid-notopterid group of isospondylous fishes. Nevertheless the Mormyriformes seems to show sufficient specializations—e.g., in the electric organ and the brain—to justify separation at the ordinal level. The controversy regarding the iniomous fishes has a somewhat different basis. Their origin in the Clupeiformes cannot be traced by more than guesswork. However, the one character usually used to differentiate the iniomous from the isospondylous fishes is the exclusion of the maxillary from the gape in the former, and Chapman (1944) and others have pointed out that various isospondylous families also have the maxillary excluded. Thus the differentiation between the two orders breaks down, and Schultz and Stern (1948) have consequently merged them. Nevertheless, it does not seem justifiable to unite two groups just because all themembers of one cannot be separated from all the members of the other by a single character. In the instance of the Myctophiformes and the Clupeiformes it is not even a question of where to draw the line in a continuous lineage, for the isospondylous fishes with the maxillary excluded from the gape (except possibly *Albula*) undoubtedly did not give rise to the iniomous fishes. But if the argument for merging the two orders seems weak, that for keeping them separate as is done here has, in this author's opinion, never been very convincingly presented. (The closest approach seems to be that of Marshall, 1955 : 305). Finally, that the haplomous fishes belong in the Clupeiformes has been convincingly argued by Berg (1936, 1940), and further evidence for this allocation has already been presented in Section 2 of this paper.

- Order Clupeiformes (Isospondyli)
  - Division I Clupei
    - Suborder I Elopoidei
      - Superfamily I Elopoidae
      - Superfamily II Albuloidae
    - Suborder II Clupeoidei
      - Superfamily I Alepocephaloidae
      - Superfamily II Clupeoidae
    - Suborder III Gonorhynchoidei
      - Superfamily I Chanoidae
      - Superfamily II Gonorhynchoidae
      - Superfamily III Phractolaemoidae
      - Superfamily IV Knerioidae
      - Superfamily V Cromerioidae

- Suborder IV Stomiatoidei
    - Superfamily I Gonostomoidae
    - Superfamily II Stomiatoidae
    - Superfamily III Astronesthoidae
- Suborder V Salmonoidei
    - Superfamily I Salmonoidae
    - Superfamily II Argentinoidae (Opisthoproctoidae)
    - Superfamily III Osmeroidae
- Suborder VI Esocoidei (Haplomi)
    - Superfamily I Dallioidae
    - Superfamily II Umbroidae
    - Superfamily III Esocoidae

Division II Osteoglossi

- Suborder VII Osteoglossoidei
    - Superfamily I Hiodontoidae
    - Superfamily II Notopteroidae
    - Superfamily III Osteoglossoidae

Certain final points regarding the classification of the isospondylous fishes presented above may be noted. First, N. B. Marshall has called my attention to the omission of three families of dubious systematic position: the Bathylaconidae (Parr, 1948), the Rosauridae (Tucker, 1954) and the Macristiidae (Regan, 1911). These are all families of oceanic fishes based on one or a few specimens. Any attempt to place them in one position or another within the Clupeiformes at the present time would be gratuitous, and it seems better to leave them *incertae sedis*. As to the better-represented groups, the classification of the superfamilies of Stomiatoidei and Esocoidei stand as they appear in Berg (1940), and the superfamily Alepocephaloidae is left as usual in the Clupeoidei. The author has almost no first hand knowledge of any of these groups.

Second, as a matter of practice this author believes that orders and suborders should be monophyletic but rather broadly interpreted. In contrast with Berg (1940), he would be very chary about the erection of orders and suborders for a few aberrant forms; these he would in general relegate to superfamilies (if such a higher category is needed). The reasoning behind this is that superfamilies are usually used by specialists, to whom the names of small divergent groups are significant, but are rarely incorporated in general classifications, where such names would generally have little meaning.

Finally, there remains the question of whether the Clupeiformes is polyphyletic. The evidence of the caudal skeleton would appear to be against such a conclusion. The caudal structures of the basal forms *Elops*, *Salmo*, *Esox*, and *Hiodon* are not only strikingly similar (Section 1), they are also widely different from anything among the recent members of the Holostei. Some of the ways in which they resemble each other and differ from the caudal skeletons of lower fishes seem to be of a type that would hardly have been developed independently twice, e.g., the three and only three hypurals to the lower caudal lobe, the peculiarities in the basal articulations of these three hypurals (No. 1 with the terminal vertebra, and Nos. 2 and 3 with the first postterminal centrum), the long uroneurals, etc. Indeed if there is any indication of polyphyletic origin in the caudal structure of the Clupeiformes it would be between the osteoglossid-notopterid stock on the one hand and *Hiodon* with all the rest of the isospondylous fishes on the other. But such a split separating *Hiodon* from the osteoglossid groups seems untenable on any other ground than the caudal skeleton.

When all features are taken into consideration only two stocks (Divisions) seem distinctly separable within the order. One of these (Division II) contains today a small number of relict forms that are all, in their peculiar fashion, mixtures of primitive and specialized characters. To exemplify the basic nature of the stock no one fish can be selected ; rather it is necessary to give a composite description based on the primitive features found in most of the Hiodontoidae, Osteoglossoidae, and Notopteroidae. If this is done it may be said that in Division II the parasphenoid remains primitive from three points of view. First, it never reaches the rear of the basioccipital ; second, it sometimes retains a pair of projections for articulation with the suspensorium ; and finally, it generally bears teeth. The last two features play a role in the general dentition and palatal construction in the stock as a whole ; in these Division II appears to have remained primitive, quite in contrast to the evolution that has occurred in Division I. Throughout Division II, except *Heterotis*, the primary portion of the bite is between the parasphenoid and the tongue (cf., Hofer, 1945). Such bony articulations as occur on the top of the mouth are between the parasphenoid and the mesopterygoid, not from the ethmoid-prefrontal area via the palatines to the maxillary pedicels. Indeed, in Division II the palatines end anteriorly in a simple point and the maxillaries merely appear to be toothed cheek bones that have come loose posteriorly ; they have no pedicels. However, if supramaxillaries are a primitive character, Division II has lost them. Also, in the vertebral column Division II would seem to have advanced farther along the road toward the fusion of elements than Division I, and in the caudal skeleton (aside from *Hiodon*) Division II seems to have evolved in a totally different way from Division I.

By contrast Division I is represented today by some primitive forms, notably the elopoids, that in most respects might stand as the ancestors of the whole division. Actually, *Elops* and *Albula* in certain characteristics, especially dentition, seem to form better prototypes for the stock than the Jurassic *Leptolepis bronni* (Rayner, 1937), for in dentition *L. bronni* seems already to have developed much of the specialization of the modern Clupeidae. Returning to modern forms, the Elopoidae and Albuloidae are the only superfamilies in the Division that have retained a parasphenoid dentition. In the others it has been totally lost, and when teeth reappear along the center of the mouth roof as in *Esox* they are on a backward projection of the vomer. The parasphenoid-mesopterygoid articulation is also lost in all modern forms though it is present in *Leptolepis bronni* (Rayner, 1937). On the other hand, a complicated cranium-palatine-maxillary articulation is usually present, giving the whole upper jaw structure an aspect rather similar to that of the higher fishes.

An important question regarding Division I is whether it contains within itself two or more independent lineages that are of equal value with Division II. One such possible independent group is the Gonorhynchidae. If, however, *Gonorhynchus* is related to *Chanos*, as is suggested in Section 3 of this paper, then its pertinence to Division I would seem fairly secure. A more moot group, in this author's opinion, is the whole salmonoid-haplomous stock. There are only two items known to the author that might serve as an indication of a salmonoid-clupeoid relationship. One is that *Albula*, which is usually assumed to be related to the clupeoids, seems to show some similarity in the caudal skeleton to that typical of the salmonoids. The other is that the stomiatoids appear to be intermediate in certain respects between the salmonoids and the clupeoids : on the one hand some of the stomiatoids have the two supramaxillaries of the clupeoid fishes and *Elops* ; on the other, many stomiatoids have the typical salmonoid adipose fin. Especially because of this puzzling link provided by the stomiatoids, it seems best to include the salmonoids in the same division with the clupeöids for the moment.

Synopsis of Modern Clupeiform Fishes to Superfamily

1a. Parasphenoid extending nearly to the posterior end of the basioccipital or beyond. Parasphenoid never with lateral processes for articulation with the mesopterygoid ; anterior ribs usually articulating with small parapophyses that are wedged into pits in the centra ; branched caudal rays often 17. Division Clupei.

2a. Teeth present on the parasphenoid ; a leptocephalous larval form. Suborder ELOPOIDEI

3a. A gular plate . . . . Superfamily ELOPOIDAE

3b. No gular plate . . . . Superfamily ALBULOIDAE

2b. No teeth on the parasphenoid ; no leptocephalous larval form.

4a. Lower intermuscular bones usually present; photophores, if present, not in two rows along lower sides ; posterior neural and hemal spines without antero-posteriorly expanded blades ; no proethmoids.

5a. Supramaxillaries usually present ; gill covers free from the isthmus ; branchiostegal rays 7 or more . . . . Suborder CLUPEOIDEI

6a. Two postterminal centra ; no temporal foramen ; black, deep-water fishes Superfamily ALEPOCEPHALOIDAE

6b. One or no postterminal centra ; a temporal foramen ; silvery, surface-living fishes . . . . Superfamily CLUPEOIDAE

5b. No supramaxillaries ; gill covers attached to the isthmus ; branchiostegal rays 3 or 4 . . . . Suborder GONORHYNCHOIDEI

7a. Scales cycloid ; gill openings not restricted ; anterior ribs articulating in part with parapophyses wedged into pits in the centra ; mouth terminal Superfamily CHANOIDAE

7b. Scales ctenoid ; gill openings not restricted ; anterior ribs articulating with strong lateral processes from the centra ; mouth inferior Superfamily GONORHYNCHOIDAE

7c Scales cycloid ; gill openings little restricted ; anterior ribs articulating directly with the centra ; mouth superior . . . Superfamily PHRACTOLAEMOIDAE

7d. Scales cycloid ; gill openings restricted ; anterior ribs articulating directly with the centra ; mouth inferior . . . . . . Superfamily KNERIOIDAE

7e. No scales ; gill openings restricted ; mouth inferior . Superfamily CROMERIOIDAE

4b. No lower intermuscular bones ; two rows of photophores along lower sides ; posterior neural and hemal spines without antero-posteriorly expanded blades ; no proethmoids . . . . Suborder STOMIATOIDEI

8a. Premaxillary without anterior expansion ; maxillary with two supramaxillaries ; gill arches with gill rakers . . . . . . Superfamily Gonostomoidae

8b. Premaxillary with a strong anterior expansion extending upward over the ethmoid; maxillary without supramaxillaries ; gill arches without normal gill rakers.

9a. Supracleithrum absent . . . . Superfamily Stomiatoidae

9b. Supracleithrum present . . . . . . Superfamily Astronesthoidae

4c. No lower intermuscular bones ; no photophores ; posterior neural and hemal spines with antero-posteriorly expanded blades (except in *Lovettia* and the Salangidae) ; proethmoids sometimes present . . . . Suborder Salmonoidei

10a. Two upturned postterminal vertebral centra . . . Superfamily Salmonoidae

10b. Not more than one upturned postterminal vertebral centrum.

11a. Oceanic fishes with small pelagic eggs. . . . Superfamily Argentinoidae.

11b. Inshore or freshwater fishes with large, demersal eggs . Superfamily Osmeroidae

4d. No lower intermuscular bones, photophores, or antero-posteriorly expanded blades on the posterior neural and hemal spines; paired proethmoids present Suborder Esocoidei

12a. Snout not greatly produced ; no canine teeth.

13a. Scapula, coracoid, and pectoral radials not ossified . . Superfamily Dallioidae

13b. Scapula, coracoid, and pectoral radials ossified . . Superfamily Umbroidae

12b. Snout greatly produced ; canine teeth present. . . Superfamily Esocoidae

1b. Parasphenoid terminating well short of the posterior end of the basioccipital. Parasphenoid sometimes with lateral processes for articulation with the mesopterygoid ; anterior ribs either articulating directly with centra or with strong parapophyses that are fused to the centra ; branched caudal rays 16 or fewer Division Osteoglossi

14a. Three or four uroneurals in the caudal skeleton ; no parasphenoid facet for articulation with the mesopterygoid ; nasals small ; symplectic a normal, splint-like bone ; basisphenoid absent ; top of skull without longitudinal ridges. Superfamily Hiodontoidae.

14b. No separate uroneurals nor parasphenoid facet ; nasals enlarged ; symplectic expanded ; basisphenoid present ; top of skull with longitudinal ridges Superfamily Notopteroidae

14c. No separate uroneurals ; parasphenoid facets present ; nasals enlarged ; basisphenoid present ; top of skull rugose but without longitudinal ridges Superfamily Osteoglossoidae

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THE ECOLOGY AND TAXONOMY OF SOME ANGOLA BIRDS

(Based on a collection made in 1957)

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BULLETIN OF
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Pp. 367–453 ; *Plates* 5–6 ; 2 *Text-figures*

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By B. P. HALL

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INTRODUCTION

SINCE Bocage published the *Ornithologie d'Angola* in 1881 no major work has appeared on the birds of the country as a whole and even the vast collection amassed by Ansorge in the early part of the century has never been fully written up. Thus little knowledge has been available to the student on the ranges and habitats of the many forms endemic to Angola although the discoveries of such collectors as Rudyerd Boulton, Gerd Heinrich and Rudolf Braun in the past twenty-five years have shown it to be a country of exceptional interest. This interest lies not only in its endemic species but also in that it is a meeting place for the avifauna of West Africa, found in the lowland forests of the west; of South West Africa, found in the coastal thorn country and desert; of East Africa, in the woodlands of the centre and east. There are also some representatives of a specialised montane avifauna in the Bailundo highlands.

Chapin's *Birds of the Belgian Congo* has done much to remedy the lack of knowledge but, of necessity, deals only briefly with Angola birds, and only with those that are found also in the Congo. In the British Museum workers have been handicapped by the paucity of specimens from Angola as well as by the lack of literature on the country, and it was with a view to filling some of the gaps in the National Collection and with learning something of the habitats and ecology of the birds, that I decided to make a collecting trip to Angola in 1957.

This paper is intended to correlate the birds that were collected with the type of country and vegetation in which they were found. For this purpose all specimens have been listed in four "Tables of Specimens Collected," divided according to their habitats, rather than in a systematic list. The main vegetation regions of the country and the particular vegetation at each camp are described and discussed in relation to the distribution of the species throughout Africa and with regard to their possible bearing on the progress of speciation. Additional notes have been made on breeding seasons and on field habits and systematics where these have proved of particular interest. The usefulness of these discussions is necessarily limited by the lack of personal knowledge of the country outside the route of the expedition and the paper as a whole is intended only to supplement the work that is being done concurrently, chiefly in the United States, on other collections from Angola, so that finally there may be a real understanding of the place of the Angola avifauna in African ornithology.

Acknowledgments

For the expedition I was fortunate to have the support of the Zoology Department, British Museum (Natural History), and in being able to get together an Anglo-American party following the Pan-African Ornithological Congress in Livingstone in July 1957. The American members were Mr. and Mrs. Donald S. McChesney, Research Associates of Cornell University. Their chief interest was in photography and sound-recording of bird songs, although they took an active interest in the specimens collected during the time they were with the rest of the expedition:

this time was unfortunately very limited as private affairs compelled them to return to the States on 2nd September. Mr. John Williams, from the Coryndon Museum, Nairobi, came to take charge of the skinning ; he also had to leave about the same time having been unluckily dogged by ill-health throughout. The chief collectors were Lt.-Gen. Sir Gerald Lathbury, K.C.B., D.S.O., M.B.E., and Mr. A. L. (Tony) Archer from Nairobi, who brought his Land Rover and Owaka and Ali as mechanic and cook. John Williams and I also collected when time allowed from skinning. During their time in Angola Mr. McChesney engaged Mr. Mario Pirelli from Luanda as an interpreter and guide to the country.

The trustees of the Percy Sladen and of the Godman Trusts made grants towards my travelling expenses and the British share of the expedition, and a grant was made from the Purchase Grant of the Museum. Further expenses were born by Mr. McChesney, General Lathbury and myself, Mr. McChesney also being responsible for the financing of the American share. The Committee of the Bird Exploration Fund contributed with the loan of a gun and the gift of some ammunition.

In Livingstone Mr. Rudyerd Boulton gave valuable advice on the country and habitats of the birds which was of great assistance in planning our route. In Angola we received unfailing help from all Government officials with whom we came in contact, and also helpful advice on the birds of the area from Mr. R. Braun at Sá da Bandeira.

Since returning to the Museum I have received great assistance in working out the collection from colleagues in the Bird Room and Mr. A. W. Exell, in the Botany Department, and through loans and letters from many ornithologists including Dr. Dean Amadon, Professor J. Berlioz, Mr. C. W. Benson, Mr. P. A. Clancey, Dr. H. Friedmann, Mr. J. C. Greenway, Mr. R. E. Moreau, Prof. N. E. Collias, Miss M. Patterson, Captain C. R. S. Pitman, Dr. A. L. Rand, Prof. H. Schouteden, Dr. W. Serle, Mr. R. H. N. Smithers, Prof. E. Stresemann, Mr. M. P. Stuart Irwin, Mr. M. A. Traylor, and Mr. C. M. N. White. Mr. Smithers also kindly had some birds skinned for me in Bulawayo which had been preserved in salt. Mr. B. C. Lack, of the Metereological Office, supplied rainfall figures. Mr. C. W. Mackworth-Praed and the late Captain C. H. B. Grant have allowed me full use of the manuscript of the second part of the African Handbook of Birds covering Southern Africa. Dr. G. Rudebeck has supplied me with a list of birds collected on the Visser-Transvaal Museum Expedition to Angola in 1956, and allowed me to examine specimens. Commander A. M. Hughes and Mrs. M. Gull have drawn the maps.

To all these people I am very much indebted, but above all to my companions for their contributions in their respective spheres, especially to the two collectors who were responsible for the unusually large variety of birds collected in two months.

Deposition of Specimens Collected

In all 980 specimens were obtained of 306 species, including the second and third known specimens of *Prionops gabela*. The majority were skinned on the spot, but some less important were preserved in salt for eventual treatment in the Museum (see Ibis, 1959 : 254), and fifty-four were preserved in spirit as anatomical specimens.

At the request of the Portuguese authorities a number of duplicate specimens have been sent to the Museum in Luanda. A proportion of the remainder, mainly from eastern districts, are in the American Museum of Natural History, a small number in the National Museum of Southern Rhodesia, Bulawayo, and the bulk in the British Museum. The photographs and sound-tracks have been deposited at Cornell University.

ITINERARY

The expedition entered Angola from the Belgian Congo along the line of the Benguela railway at Dilolo. It had been hoped to do some exploratory work in the little known areas of the east and south-east, but Williams' illness and shortage of time made this impossible. Thus little new ornithological ground was broken except in some parts along the main road from the frontier to Nova Lisboa, and energies were mostly concentrated on seeing as many different types of country as possible, and in filling the known gaps in the British Museum collection from such well-known districts as Mt. Moco, Sá da Bandeira, Chingoroi and Gabela.

A full list of camps follows with the altitudes and dates so that these may be correlated with the Tables of Specimens collected at the different camps :—

Date of arrival	Locality of camp	Lat.	Long.	Alt.
27th July	Luau R. Angola/Congo border 7 m. E. of Texeira de Souza	10.42 S.	22.12 E.	3,600′
1st August	Luacano	11.16 S.	21.38 E.	3,550′
3rd ,,	Lake Dilolo	11.30 S.	22.00 E.	3,500′
6th ,,	Luacano	—	—	—
7th ,,	28 m. W. of Vila Luso	11.47 S.	19.52 E.	4,400′
8th ,,	5 m. W. of Munhango	12.12 S.	18.42 E.	4,700′
9th ,,	5 m. W. of Vila General Machado	12.03 S.	17.30 E.	4,800′
10th ,,	Vouga	12.11 S.	16.47 E.	5,700′
12th ,,	5 m. E. of Nova Lisboa	12.44 S.	15.47 E.	5,500′
14th ,,	Mt. Moco	12.27 S.	15.10 E.	6,000–8,000′
25th ,,	5 m. N. of Vila Flor	12.41 S.	15.31 E.	5,500′
27th ,,	Caconda	13.43 S.	15.06 E.	5,200′
28th ,,	Quipungo	14.49 S.	14.34 E.	4,400′
29th ,,	Sá da Bandeira	14.55 S.	13.30 E.	5,600′
30th ,,	Leba	15.04 S.	13.16 E.	5,800′
4th September	Cahinde (Tampa)	15.30 S.	13.27 E.	2,500′
6th ,,	5 m. S.W. of Sá da Bandeira	—	—	6,600′
7th ,,	Chingoroi	13.37 S.	14.01 E.	3,300′
11th ,,	12 m. S.E. of Benguela	12.35 S.	13.25 E.	S.L-500′
13th ,,	60 m. N. of Lobito on Novo Redondo road	—	—	*c.* 800′
14th ,,	20 m. N.E. of Novo Redondo on Gabela road	—	—	*c.* 1,000′

Date of arrival	Locality of camp	Lat.	Long.	Alt.
15th ,,	Cuvo R. 12 m. S.W. of Gabela	10.48 S.	14.20 E.	2,500′
20th ,,	40 m. S. (by road) of Mumbondo	10.09 S.	14.15 E.	1,000′
25th ,,	Calulo	10.00 S.	14.53 E.	3,300′
27th ,,	Quimberima plantation 40 m. S.E. of Calulo	—	—	3,700′
Other localities by roadside:				
9th August	Coemba, 40 m. W. of Munhango	—	—	—
	Saiangikilo R. 16 m. W. of Munhango	—	—	—
13th ,, and 25th	Quipeio, 25 m. N.W. of Nova Lisboa	12.26 S.	15.30 E.	c. 6,000′
7th September	Quilengues, on Sâ da Bandeira-Chingoroi road	14.00 S.	14.00 E.	c. 3,900′

VEGETATION

Main Vegetational Regions

All the main vegetation regions of tropical Africa are represented in Angola with the exception of extensive marshlands of the "Sudd" type. These regions are indicated on the following map which has been adapted from the Vegetation Map of Africa published on behalf of l'Association pour l'Étude Taxonomique de la Flore d'Afrique Tropicale with the assistance of U.N.E.S.C.O. (Oxford University Press: 1959), with slightly more detail in those districts covered by the expedition. The regions can be summarized as follows :—

(a) *Savannah Woodland*

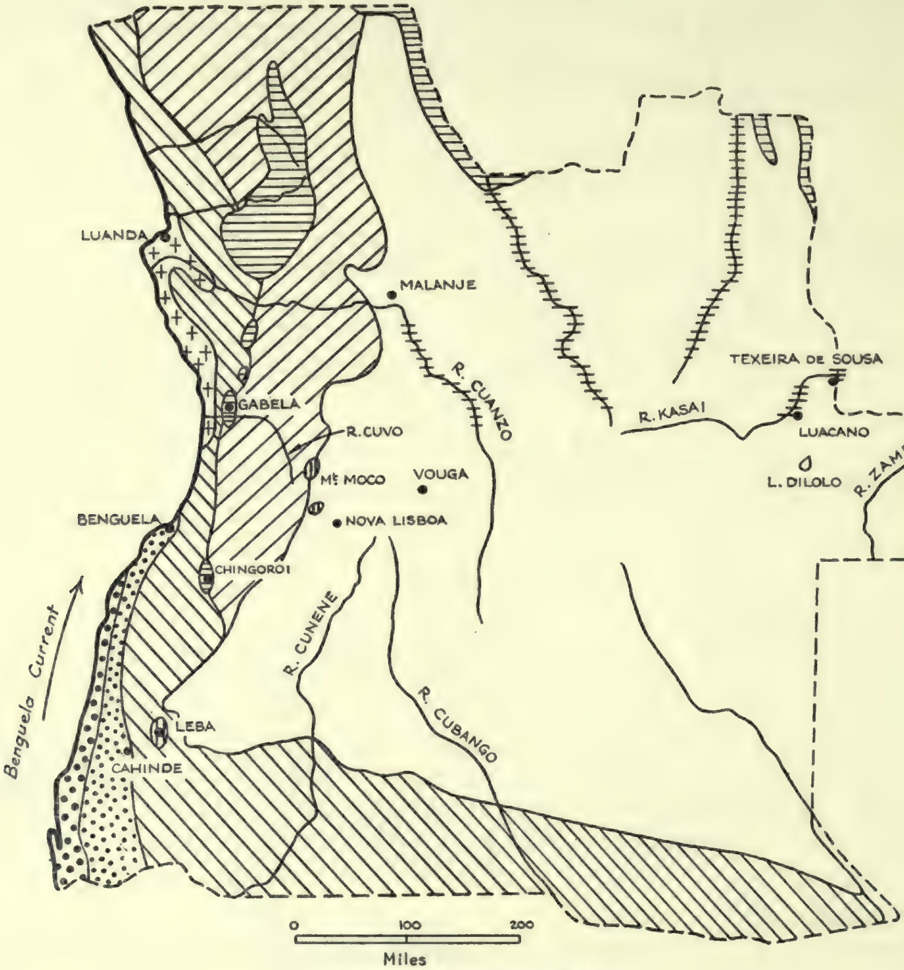
In eastern and central Angola this is largely of the *Brachystegia* and *Isoberlinia* type and is extensive, being found even up to 7,000 feet on the mountain slopes. For convenience it will be referred to throughout as Brachystegia woodland.

In the west, in a narrow strip along and below the escarpment, there is rather richer vegetation, shown on the map as relatively moist types of savannah woodland. In this strip Brachystegia no longer predominates, there is more variety and Baobabs are common.

(b) *Grassland*

Patches of grassland often very flat and poorly drained are interspersed throughout the Brachystegia woodland. In the west there is more open country with many wide stretches of rolling grassland in which other vegetation is confinen to thickets and clumps, mostly in the river and stream valleys.

VEGETATION MAP OF ANGOLA


LUANDA
MALANJE
R. CUANZO
TEXEIRA DE SOUSA
R. KASAI
LUACANO
L. DILOLO
R. ZAMBESI
GABELA
R. CUVO
Mt MOCO
VOUGA
NOVA LISBOA
BENGUELA
CHINGOROI
R. CUNENE
R. CUBANGO
LEBA
CAHINDE
Benguela Current
0
100
200
Miles

KEY TO VEGETATION MAP

▥	Montane Forest
▤	Escarpment or Riverine Forest
▨	Mixed Woodlands and Savannahs relatively moist types
▧	Mixed Woodlands and Savannahs, relatively dry types with abundant Acacia
□	Woodlands and Savannahs with abundant Brachystegia
+ + +	Grass Steppe, Luanda type
⁘	Semi-desert
⁙	Desert

(c) *Semi-desert and Thorn*

In the south and south-west the acacia thornveld of the Kalahari and South West Africa extends into Angola and along the coastal strip to the latitude of Lobito. Here the sandy plain gives way to the rolling grassland and the predominance of acacia diminishes northwards to Luanda.

(d) *Desert*

The Namib desert of South West Africa extends in a narrow strip up the coastal plain into southern Angola, merging into the semi-desert or scrub a little north of Moçamedes and in the foothills towards the base of the Chela escarpment.

(e) *Forest*

The forests of Angola, excluding Cabinda in which true tropical rain forest is found, are of three types. True montane forest of great antiquity is found in pockets on the highest mountains of the Bailundo highlands such as Mt. Moco and Mt. Soque. It was also fairly extensive on the Mombolo plateau when Boulton collected there in 1931, but we were informed in Nova Lisboa that it has largely been cut down. Remnants of forest on the Chela escarpment may also prove to be relic montane type.

The lowland forests are of more recent origin and can be divided into what might be termed escarpment forest, and gallery or riverine forest. The escarpment forest is found between 1,000 feet and 3,000 feet in sometimes extensive patches below or on the face of the escarpment in areas which combine the high summer rainfall of inland districts with high all-the-year-round humidity and frequent mists due to the meeting of the cold waters of the Benguela current with the warm equatorial waters.

Gallery forest is found in patches along the rivers of the north and east, and also along some of the west coast rivers below the escarpment.

Vegetation at Camps

The expedition traversed all the main vegetation regions with the exception of the true desert and it seems useful to discuss in more detail the country at each camp, and on the road between. The camps and districts discussed have been numbered to correspond with the columns in the Tables of Specimens collected (pages 379–391).

(1) *Luau River*

Most of the collecting was done in the narrow strip of riverine forest or the Brachystegia woodland around. There was no open grassland but some clearings in the woodland and the edges of cultivation.

(2) *Luacano Area*

There was some riverine forest and Brachystegia woodland, but the camp was chiefly notable for the wide flat treeless plain crossed by damp ditches which extended some miles east and south of Luacano village.

(3) *Lake Dilolo*

Most of the collecting was done in the grassy swamps and reed-beds on the border of the lake near the Government Rest House, and a little in some woodland a few miles to the west. There was no time to explore the extensive possibilities of the lake, the largest in Angola, or to organize the use of native dugout canoes which would be the most suitable transport for the purpose.

(4) *Roadside Localities between Luacano and Vouga*

All camps were made in Brachystegia woodland but this was interspersed with grassy dambos similar to the grassland at Luacano in their flatness and lack of bushes, but not so extensive. (Plate 5, B).

(5) *Vouga*

The grasslands here differed in being extensive undulating plains with moist marshy patches in the valleys and some patches of scrubby bushes. A small patch of stunted woodland with some bushes and cultivation surrounded the camp.

(6) *Nova Lisboa area*

This area was predominantly Brachystegia woodland with some grassy clearings and cultivation.

(7) *Foothills of Mt. Moco*

The lower slopes were covered with Brachystegia woodland with thick tangled grasses in the stream beds, and grassland and cultivation below.

(8) *Mt. Moco, over* 6,000 *feet*

Brachystegia was found up to 7,000 feet on some slopes and montane forest was limited to patches lining precipitous gullies at the head of the streams on the upper slopes, descending to about 6,800 feet on some of the eastern and southern slopes. The forest trees were nowhere very tall or very dense but mostly of evergreen species totally different from the woodland types and with tangled undergrowth beneath. The bare slopes above the woodland and away from the forest were rocky and grassy with scattered aloes and small scrub, with numerous plants in flower.

(9) *Vila Flor, and localities on Luimbale-Nova Lisboa road*

This area was predominantly Brachystegia woodland with some grassy clearings and cultivation.

(10) *Caconda and Caconda-Quipungo road*

This country was similar to Vila Flor until a change was noted about 40 miles south of Caconda where the trees appeared much the same size and form but were notably barer of leaves. This change would not have been worthy of note except that it corresponded with some change in the bird life, four species being met within a few miles which had not hitherto been encountered, namely, *Neocichla gutturalis*, *Thamnolea arnotti*, *Turdoides jardinei* and *Eurocephalus anguitimens*.

(11) *Quipungo*

The first patch of thorn country was encountered here, with some grassy clearings and a small patch of Brachystegia.

(12) *Sá da Bandeira and the roads to Quipungo and Chingoroi*

This was very mixed country with thorn and Brachystegia alternating, and with richer and more varied vegetation northwards towards Chingoroi as the road descends to 3,000 feet. An overnight camp at Sá da Bandeira was made on top of the escarpment above the town and some collecting was done in the stunted Brachystegia on the slopes and the rocks above.

(13) *Leba and Humpata-Jau road*

The camp at Leba was in an area of mixed vegetation. It was situated about a mile inland from the edge of the Chela escarpment at a point where a stream cuts its way through a gorge in a series of waterfalls down 3,000 feet to the foothills and plains at Capangombe. Immediately around the camp was an area of tangled bush and thorn full of aromatic shrubs ; in some clearings by the river were remnants of forest and a patch of forest was found by the river near the foot of the escarpment.

The rocks and fringing trees of the escarpment were the typical habitat of *Xenocopyschus ansorgei*, and in one place along the edge was an extensive patch of tangled evergreen bush, difficult to penetrate, which contained few birds. Other slopes above the river were covered in stunted Brachystegia, and on the plateau running back from the escarpment patches of Brachystegia were mixed with patches of thorn and occasional grassy or cultivated clearings. (Plate 5, A).

In such mixed country it was not always easy to define the habitat of specimens collected and this should be borne in mind when consulting the Tables.

Some collecting of larks and pipits was done on open grassland on the Humpata-Jau road, and a party of water-birds was seen at a small lagoon in the centre of these grasslands.

(14) *Cahinde area*

Included in this area, is the road down the escarpment where the slopes are lined with stunted Brachystegia and Mopane. This gives way at the bottom of the escarpment among the foothills to typical semi-desert country of mixed thorn and *Terminalia* or *Combretum*, with the Mopane becoming less common westwards towards the desert. An excursion was made westwards for fifty miles from Cahinde without coming out of the foothills into true desert.

(15) *Chingoroi*

The patch of forest in which most of the collecting was done might be described as part riverine and part escarpment being associated with a stream, but more extensive than the usual riverine strips. Other birds were collected in reeds and grasses bordering the stream.

(16) *Benguela area* (3–15 *Miles South-east*)

The descent from Chingoroi to the coastal strip behind Benguela was gradual and through mixed country which gave way on the coastal plain to typical thorn bush resembling the Kalahari and the Vornamib. It was more open than the country at Cahinde with more grassland and acacia and no Mopane, and only broken by rocky kopjes.

(17) *Lobito—Novo Redondo-Gabela road*

The road to Novo Redondo wound over the rolling grasslands mentioned in the discussion on vegetational regions. Thorn bushes and Euphorbia were found on the hill-sides and frequent clumps of dry tangled thickets similar to those found on above the escarpment at Leba. Baobabs were common. Between Novo Redondo and the foot of the escarpment there were clumps of richer vegetation bordering streams and lagoons, but no collecting was done here.

(18) *Cuvo River,* 12 *Miles SW. of Gabela*

All collecting from this camp was done within three or four miles of the river and in the forest on the face of the escarpment, which is again precipitous at this latitude, though not to such a degree as at Leba. The forest is largely underplanted with coffee and the original undergrowth destroyed, but there was an uncleared patch in which we collected not far from the camp. The forest ended abruptly at the top of the escarpment before the town of Gabela and also a few miles further south along the road beyond our camp. The few species listed as collected in grassland in this camp were from tangled grass near the river's edge or a patch of disused cultivation in a forest clearing.

(19) 40 *Miles South of Mumbondo and road to Luanda*

Very little collecting was done on the road from Gabela to Luanda via Mumbondo and Muxima, but it was noteworthy for finding *Prionops gabela* well outside the forest area at the foot of the escarpment in a patch of mixed bush and woodland between cultivated clearings.

(20) *Calulo and Quimberima* (40 *Miles SE. of Calulo*)

After the main expedition was over I collected a few birds at Calulo which is situated in open grassland with some patches of stunted Brachystegia and bush, and on the plantation of Mr. and Mrs. O. Kroel at Quimberima, where they very kindly put me up for two nights. The Quimberima birds were collected in a tiny patch of forest edging a stream and bordered by Brachystegia.

Photographs

Photographs and further descriptions of many of the localities and types of vegetation discussed will be found in Lynes' two papers on his expeditions to Angola (1933 and 1938), in Heinrich's recent paper (1958), and in Gosswelier & Mendonca (1939).

TABLES OF SPECIMENS COLLECTED

Key to Tables

Species which appear in more than one table, or which are referred to in the Systematic and Field Notes, have cross references in the left hand columns.

Collecting localities are grouped into districts for estimate of breeding dates and numbered as follows :

1. Luau R.
2. Luacano area : Texeira de Sousa—Luacano road.
3. Lake Dilolo.
4. Vila Luso—Vouga road.
5. Vouga.
6. Nova Lisboa area.
7. Foothills of Mt. Moco (6,000 feet).
8. Mt. Moco over 6,000 feet.
9. Vila Flor : Quipeio : Nova Lisboa—Luimbale road.
10. Caconda : Caconda—Quipungo road.
11. Quipungo.
12. Sá da Bandeira : Sá da Bandeira—Quipungo road : Sá da Bandeira—Chingoroi road.
13. Leba : Humpata—Jau road.
14. Cahinde : road down escarpment : Cahinde—Moçamedes road (40 miles).
15. Chingoroi.
16. Area 3—12 miles S.E. of Benguela.
17. Lobito—Novo Redondo—Gabela road.
18. Cuvo R., 12 miles S.E. of Gabela.
19. Forty miles south of Mumbondo.
20. Calulo : Quimberima (40 miles S.E. of Calulo).

Unsexed specimens are listed by number only (i.e. 1 ♂, 2 ♀, 1).
Specimens in spirit are listed in brackets.
Young birds not fully grown are listed as " juv."
Young birds fully grown are listed as " imm."
" Summer " breeding season indicates any month between November and May.

TABLE I.—*Birds*

	Other references		Eastern Districts				Central		
	Tables	Syst. Notes	1	2	3	Breeding	4	5	6
4 Francolinus finschi	—	*	—	—	—	—	—	—	—
6 coqui angolensis	—	—	—	—	—	—	—	—	1 ♂
15 Chrysococcyx klaasi	—	—	—	(1 ♀)	—	—	—	—	—
16 Cuculus c. cafer	—	—	—	—	—	—	1 ♂	—	—
19 Poicephalus meyeri damarensis	II	—	—	—	—	—	—	—	—
24 Coracias spatulatus	—	—	—	1 ♂	—	Summer	—	—	—
25 Halcyon chelicuti	—	—	—	(1)	—	—	—	—	—
28 Merops nubicoides	—	—	—	1 ♂	—	? Sept.	—	—	—
29 Melittophagus pusillus meridionalis	—	—	—	—	—	—	—	—	—
30 Dicrocercus h. hirundineus	—	—	1 ♂	—	(1)	Summer	—	—	—
31 Tockus p. pallidirostris	—	—	1 ♂	—	—	—	—	—	—
34 Glaucidium perlatum licua	—	—	—	—	—	—	—	—	—
37 Semeiophorus vexillarius	—	—	—	—	—	—	—	1 ♂	—
40 Caprimulgus pectoralis fervidus	—	—	3 ♀	—	—	Summer	—	—	—
45 Colius striatus congicus	—	*	1 ♂	—	—	? Aug.	—	—	—
47 castanotus	II, IV	*	—	—	—	—	—	—	—
48 Lybius torquatus bocagei	—	*	1 ♂, 1 ♀	—	—	? July onwards	—	—	—
49 Buccanodon anchietae anchietae	—	*	—	—	—	—	—	—	—
rex	—	—	—	—	—	—	—	—	—
katangae	—	—	—	—	1 ♂	Summer	1 ♂, 1 ♀	—	—
52 Tricholaema diadematum frontatum	—	—	—	—	—	—	—	—	—
54 Pogonolius chrysoconus extoni	IV	—	—	—	2 ♀	? Aug./Sept.	—	—	—
56 Prodotiscus regulus	—	—	1 ♂, 1 ♀	—	—	—	—	—	—
57 insignis lathburyi	—	—	—	—	—	—	—	—	—
59 Campethera cailliautii fulleborni ⪌ permista	—	*	1 ♂	—	—	? June	1 ♀	—	—
61 Dendropicos fuscescens hartlaubii	IV	*	1 ♂	1 ♀	—	? Sept. onwards	—	—	—
62 Mesopicos griseocephalus persimilis	—	*	—	—	—	—	—	—	—
76 Anthus similis schoutedeni	—	*	—	—	—	—	—	—	—
77 lineiventris	—	*	—	—	—	—	—	—	—
82 Turdoides jardinei tamalakanei	—	—	—	—	—	—	—	—	—
94 Alseonax adustus angolensis	—	—	—	—	—	—	1 ♂, 1 ♀	—	—
angolensis ⪌ subadustus	—	—	1 ♀	—	—	? Sept.	—	—	—
97 Myopornis böhmi	—	—	—	—	—	—	1 ♂	—	—
101 Bradornis pallidus murinus	IV	—	—	—	—	—	1 ♂, 1 ♀	—	—
103 Melaenornis pammelaina	—	—	—	—	—	—	1 ♀	—	—
105 Hyliota australis slatini (?)	—	*	—	—	—	—	3 ♂, 1 ♀	—	—
106 flavigaster barbozae	III	—	—	—	—	—	1 ♂	—	—
107 Batis m. molitor	—	—	1 ♂	(2 ♀)	(1 ♂), 1 ♀	? Sept.	—	—	—
111 Platysteira peltata mentalis	II	—	—	1 ♀	—	Summer	—	—	—
113 Elminia albicauda	II	—	—	1 ♀	—	—	—	—	—
114 Tchitrea viridis plumbeiceps	II	*	—	—	—	—	—	1 ♂, 1♀	—
116 Turdus libonyanus verreauxi	—	—	1 ♂	—	—	? Sept.	—	—	—
119 Geokichla litsipsirupa stierlingi	—	*	—	—	—	—	1 ♀	—	—
120 Monticola angolensis	—	—	—	—	—	—	—	—	—
124 Cercomela familiaris falkensteini	IV	—	—	—	—	—	—	—	—
125 Myrmecocichla arnotti harterti	—	—	—	—	—	—	—	—	—
137 Erythropygia b. barbata	—	—	—	—	—	—	1 ♂	—	—
147 Calamonastes simplex huilae	—	*	—	—	—	—	—	—	—
152 Sylvietta r. ruficapilla	—	*	—	—	1♀	? Oct.	—	—	—
155 Eremomela icteropygialis polioxantha	IV	—	—	—	—	—	1	1	—
156 Eremomela scotops pulchra	—	—	—	—	1 ♂ (2)	? Sept.	1 ♂	—	—
157 atricollis	—	—	—	—	—	—	2 ♂	—	—
158 salvadorii	—	*	—	—	—	—	—	—	—
159 Camaroptera brevicaudata subsp.?	II, IV	*	1 ♂ (1)	—	—	—	—	—	—
162 Cisticola chiniana fortis	IV	—	—	—	—	—	—	—	—
166 fulvicapilla dispar	IV	—	—	—	—	—	—	—	—
dispar ⪌ hallae	—	—	—	—	1 ♂	Summer	—	—	—
177 Prinia subflava graueri	IV	—	—	—	1 ♂	Summer	—	—	—
179 flavicans bihe	IV	—	—	—	—	—	—	2 ♂, 2 ♀	—
191 Psalidoprocne orientalis reichenowi	—	—	2 ♂ (1)	1 imm. ♂	—	? June	—	—	—
195 Coracina pectoralis	—	—	1 ♀	—	—	Summer	—	—	—
197 Prionops plumata poliocephala	—	—	—	—	1 ♂	? June	1	—	—
198 retzii nigricans	—	—	—	—	—	—	1 ♂	—	—
200 Eurocephalus anguitimens	—	—	—	—	—	—	—	—	—
201 Nilaus afer affinis	—	—	—	—	—	—	—	—	1 ♂
202 Lanius s. souzae	—	—	—	1 ♂	—	Summer	—	1 ♂	1 ♂
205 Laniarius aethiopicus major	—	*	1 imm. ♂	1 ♂	—	? May/June	—	—	—
208 Dryoscopus cubla hamatus	II, IV	—	—	—	—	—	1 ♂	—	—
211 Tchagra s. senegala	—	*	1 ♂, 1 ♀	1 ♀	—	? June	—	—	—
213 Antichromus minutus anchietae	—	—	1 ♀	—	—	—	—	—	—
216 Chlorophoneus sulfureopectus similis	II	—	—	1 ♂, 1	—	—	—	—	—
218 Malaconotus hypopyrrhus interpositus	—	*	1 ♂	—	—	? June	1 ♀	—	—
222 Parus leucomelas insignis	IV	—	1 ♂	—	—	Summer	—	—	—

of the Woodlands

Districts				Mt. Moco		South-central and South-western Districts						
7	9	20	Breeding	8	Breeding	10	11	12	13	15	Breeding	
—	—	—	—	1 ♂, 1 ♀	? Sept.	—	—	—	—	—	—	4
—	—	—	? June	—	—	—	—	—	—	—	—	6
—	—	—	—	—	—	—	—	—	—	—	—	15
—	—	—	Summer	—	—	—	—	—	—	—	—	16
—	—	—	—	—	—	—	—	1 ♂	—	—	—	19
—	—	—	—	—	—	—	—	—	—	—	—	24
—	—	—	—	—	—	—	—	—	—	—	—	25
—	—	—	—	—	—	—	—	—	—	—	—	28
—	1 ♀	—	Summer	—	—	—	—	—	—	—	—	29
—	—	—	—	—	—	—	—	—	—	—	—	30
—	—	—	—	—	—	—	—	—	—	—	—	31
—	—	—	—	—	—	—	—	—	1 ♀,	—	—	34
—	—	—	Summer	—	—	—	—	—	—	—	—	37
—	—	—	—	—	—	—	—	—	—	—	—	40
—	—	—	—	—	—	—	—	—	—	—	—	45
1 ♂, 2 ♀, 1 juv. ♂	—	—	July	—	—	—	—	—	—	—	—	47
3 ♂	—	—	July/Aug.	—	—	—	—	—	—	—	—	48
—	—	—	—	—	—	1	—	—	—	—	—	49
1 ♂	—	—	? June	—	—	—	—	—	—	—	—	
—	—	—	? Sept.	—	—	—	—	—	—	—	—	
—	—	—	—	—	—	1 ♂	—	—	—	—	Summer	52
1 ♂	2 ♂	—	? Oct.	—	—	—	—	1 ♂	—	—	? July	54
—	—	—	—	—	—	—	—	—	—	—	—	56
—	—	—	—	1 ♀	? Sept.	—	—	—	—	—	—	57
—	—	—	—	—	—	—	—	—	—	—	—	59
—	1 ♀	—	Summer	—	—	1 ♂	—	—	—	—	Summer	61
—	—	—	—	—	—	—	—	—	1 imm.	—	—	62
1	1	—	—	—	—	1 ♂	—	—	—	—	? Oct.	76
—	—	—	—	1 ♂	Summer	—	—	—	—	—	—	77
—	—	—	—	—	—	1 ♂, 1 ♀	—	—	—	—	Summer	82
—	—	—	—	1 ♀	? Sept.	2	—	1 ♂	—	—	? Oct.	94
—	—	—	—	—	—	—	—	—	—	—	—	
—	1 ♂	—	? Sept. onwards	—	—	—	—	—	—	—	—	97
1 ♂	—	—	? July onwards	1 ♂	Summer	—	—	—	—	—	—	101
—	—	—	? July	—	—	—	—	—	—	—	—	103
—	—	—	? Sept.	—	—	—	—	—	—	—	—	105
1 ♂	—	—	? Sept.	—	—	—	—	—	—	—	—	106
1 ♂, 1 ♀	1 ♂	—	? Sept.	—	—	—	—	—	—	—	—	107
—	—	—	—	—	—	—	—	—	—	—	—	111
—	—	—	—	—	—	—	—	—	—	—	—	113
—	—	—	? Aug.	—	—	—	—	—	—	—	—	114
1 ♀	1 ♂, 1 ♀	—	? Sept.	—	—	—	—	—	—	—	—	116
—	—	—	? Sept.	—	—	—	—	—	—	—	—	119
—	—	1 imm. ♂	? May/June	—	—	—	—	—	—	—	—	120
—	—	—	—	1 ♂, 1 ♀	? Sept.	—	—	—	—	—	—	124
—	—	—	—	—	—	2 ♂, 1 ♀	—	2 ♂	—	—	? Sept.	125
—	1 ♀	—	? Sept. onwards	—	—	—	—	—	—	—	—	137
1 ♀	1 ♀	—	? Sept.	—	—	—	—	—	—	—	—	147
—	1 ♂	—	? Oct.	—	—	1 ♀	—	—	—	—	? Oct.	152
—	—	—	—	—	—	—	—	—	—	—	—	155
(1)	1 ♂ (3)	—	? Sept.	—	—	—	—	—	—	—	—	156
—	1 ♂, 1 ♀	—	? Sept. onwards	—	—	1 ♀	—	—	—	—	? Sept.	157
—	1 ♀	—	? Sept.	—	—	—	—	—	—	—	—	158
—	—	—	—	—	—	—	—	—	—	—	—	159
—	—	—	Summer	—	—	—	—	—	—	—	—	162
—	2 ♂	—	Summer	—	—	—	—	—	—	—	—	166
—	—	—	—	—	—	—	—	—	—	—	—	
1 ♂, 1 ♀	(1)	—	? July onwards	1 imm. ♀	? May/June	—	—	—	—	1 ♂	? July	177
—	—	—	? Sept. onwards	—	—	—	—	—	—	—	—	179
1 ♂	—	—	? June	—	—	—	—	—	—	—	—	191
—	—	—	—	—	—	—	—	—	—	—	—	195
—	—	—	—	—	—	—	2 ♀	—	—	1	? July	197
—	—	—	? Oct.	—	—	—	—	—	—	—	—	198
—	—	—	—	—	—	1 ♂	—	—	—	—	—	200
1 ♂, 1 ♀	1 ♂, 1 ♀	—	? Sept.	—	—	—	—	—	—	—	—	201
—	—	—	Summer	1 ♂	Summer	—	—	—	—	—	—	202
—	—	—	—	—	—	—	—	—	—	—	—	205
—	—	—	—	—	—	—	—	—	—	—	—	208
1 ♀	—	—	? June	—	—	—	—	—	—	—	—	211
—	—	—	—	1	—	—	—	—	—	—	—	213
—	—	—	—	—	—	—	—	—	—	—	—	216
—	—	—	? Sept.	—	—	—	—	—	—	—	—	218
—	—	1 imm. ♀	? May/June	—	—	—	—	—	—	—	—	222

TABLE I.—

	Other references		Eastern Districts				Central		
	Tables	Syst. Notes	1	2	3	Breeding	4	5	6
223 Parus r. rufiventris	—	—	—	1 ♂	—	? Sept.	—	—	—
224 Oriolus auratus notatus	—	—	1 ♂	—	—	? June	1 ♂	—	—
225 Neocichla g. gutturalis	—	—	—	—	—	—	—	—	—
226 Cinnyricinclus leucogaster verreauxi	—	—	1 ♂	—	—	? June	—	—	—
228 Lamprotornis mevesii benguelensis	IV	*	—	—	—	—	—	—	—
229 acuticaudus	II	—	—	1 ♂	—	? Aug.	1 imm. ♀	—	—
231 Zosterops senegalensis quanzae	—	*	—	—	—	—	—	—	—
heinrichi	II	—	—	—	—	—	1 ♂	—	—
quanzae ≷ anderssoni	—	—	—	—	—	—	—	—	—
232 Nectarinia kilimensis gadowi	—	*	—	—	—	—	—	—	1 ♂, 1 ♀, 2 imm. ♂, 1 imm.
233 bocagei	—	*	—	—	—	—	—	—	—
235 Cinnyris cupreus chalceus	—	—	1 ♀	(1)	1 ♂	Summer	1 ♀	—	2 ♂ (1)
237 o. oustaleti	—	*	—	—	—	—	—	1 ♂	1 ♀, 1 imm. ♀
238 venustus falkensteini	—	—	—	2 ♂, 1 imm. ♂	—	? June onwards	1 ♂	—	(2)
239 afer ludovicensis	II	—	—	—	—	—	—	—	—
240 chalybeus intermedius	—	—	—	—	—	—	(2)	—	—
242 Chalcomitra amethystina deminuta	—	—	2 ♂ (1)	—	—	? June	3 ♂	2 ♀	—
243 senegalensis saturatior	—	—	—	1 ♂	1 ♂, 1 ♀	? June	1 ♂	—	1
246 Anthreptes collaris phillipsi	II	*	—	—	1 imm. ♂ 1 imm. ♀	June	1 ♂	—	—
247 longuemariae angolen-	—	—	1 ♂	—	—	? Sept.	—	—	—
248 anchieti	—	—	—	—	—	—	—	—	—
249 Salpornis spilonota salvadori	—	—	—	—	—	—	1 ♂	—	—
254 Petronia superciliaris	—	—	1 ♀	—	1 ♂	? Sep	1 ♂	—	—
258 Ploceus x. xanthops	II	—	—	—	—	—	—	—	—
269 Lonchura cucullata scutata	—	—	(1)	—	—	—	—	—	—
274 Pytelia m. melba	IV	—	—	—	—	—	—	—	1 ♂
289 Steganura paradisaea obtusa	—	—	1 ♀	—	—	? Aug.	1 ♂	—	—
291 Serinus sulphuratus sharpii	—	—	—	—	—	—	—	—	1
295 Poliospiza gularis benguellensis	—	—	—	—	—	—	—	—	—
297 Emberiza cabanisi cognominata	—	—	—	—	—	—	1 ♂	—	—
298 f. flaviventris	IV	—	2 ♂, 1 imm. ♂	—	—	? May/June	—	—	—

TABLE II.—*Birds*

	Other references		Eastern Districts (riverine)		
	Tables	Syst. Notes	1	2	Breeding
1 Accipiter minullus	—	—	—	—	—
2 Francolinus swierstrai	—	*	—	—	—
14 Turtur tympanistria fraseri	—	—	—	—	—
17 Ceuthmochares a. aereus	—	—	—	—	—
19 Poicephalus meyeri matschei	I	—	—	1 ♂	—
21 Tauraco corythaix schalowi	—	*	—	—	—
22 erythrolophus	—	*	—	—	—
27 Ispidina p. picta	—	—	1 ♂	—	—
36 Ciccaba woodfordii bohndorffi	—	—	1 ♂	—	Summer
41 Caprimulgus poliocephalus koesteri	—	*	—	—	—
43 Heterotrogon vittatus camarunensis	—	*	—	—	—
44 Apaloderma n. narina	—	*	—	—	—
47 Colius castanotus	I, IV	*	—	—	—
50 Gymnobucco calvus vernayi	—	*	—	—	—
53 Viridibucco coryphaea angolensis	—	*	—	—	—
55 Indicator m. minor ≷ conirostris	—	*	1 ♂	—	? July
58 Campethera abingoni annectens	IV	—	1 ♀	—	Summer
60 nivosa herberti	—	*	—	—	—
62 Mesopicos griseocephalus persimilis	I	*	—	—	—
63 Smithornis capensis albigularis	—	—	2 ♂, 1 ♀	—	—
83 Pseudoalcippe abyssinicus ansorgei	—	—	—	—	—
84 Malacocincla fulvescens dilutior	—	*	—	—	—
86 Pycnonotus barbatus tricolor	—	—	—	—	—
87 Andropadus l. latirostris	—	—	—	—	—
88 virens zombensis	—	—	2 ♂	1 ♂, 1 ♀	? June

Continued

Districts				Mt. Moco		South-central and South-western Districts						
7	9	20	Breeding	8	Breeding	10	11	12	13	15	Breeding	
—	—	—	—	—	—	—	—	—	—	—	—	223
—	—	—	? Aug.	—	—	—	—	—	—	—	—	224
—	—	—	—	—	—	2 ♂, 2 ♀ (1)	—	—	—	—	Summer	225
1 ♂	—	—	? July	—	—	—	—	—	—	—	—	226
—	—	—	—	—	—	—	—	1 ♀	—	—	Summer	228
1 ♂, 1 ♀	—	—	? May/June and Sept.	—	—	—	—	—	—	—	—	229
—	1 ♀	—	? Sept.	1	—	—	—	—	—	—	—	231
—	—	—	? July	—	—	—	—	—	—	—	—	
—	—	—	—	—	—	—	—	—	1 ♂	—	? July	
5 ♂, 1 imm. ♂	1 ♂ (1)	—	June	4 ♂, 1 ♀ (1)	? July	—	—	—	—	—	—	232
—	1 ♂, 1 ♀ 3 imm. ♀	—	June	—	—	—	—	—	—	—	—	233
—	(3)	—	Summer	(1)	—	—	—	—	—	—	—	235
4 ♂, 1 juv. (1)	2 ♂, 2 imm. ♀	—	June onwards	—	—	—	—	—	—	—	—	237
—	1 ♀	—	Summer	—	—	—	—	—	1 ♂	—	—	238
—	—	—	—		—	—	—	1 ♀	—	—	—	239
1 ♂		—	—	—	—	1 imm. ♂. 1 ♀	—	—	—	—	—	240
—	1 ♂, 1 ♀ 1 imm. ♂ (1)	—	June	1 ♂	? June	—	—	—	—	—	—	242
1	1 imm. ♂	—	? June	—	—	—	—	—	—	—	—	243
—	—	—	—	—	—	—	—	—	—	—	—	246
—	1 ♀, 1 imm. ♂	—	—	—	—	1 ♂, 1 imm. ♂	—	—	—	—	—	247
1 ♀	2 ♂	—	? June	—	—	—	—	—	—	—	—	248
2 ♂	—	1 ♂	? Sept.	—	—	—	—	1 ♂	—	—	? Aug.	249
1 ♂	1 ♂	—	? Sept.	—	—	—	—	—	—	—	—	254
1 ♂, 1 ♀	—	—	? Sept.	1 ♀	? Sept.	—	—	—	—	—	—	258
1	—	—	—	(1)	—	—	—	—	—	—	—	269
—	—	—	? July	—	—	—	—	—	—	—	—	274
—	—	—	? Aug.	—	—	—	—	—	—	—	—	289
2 ♂	—	—	? July onwards	1 ♂	? July	—	—	—	1 ♂	—	—	291
—	—	—	—	1 ♀	? Sept.	—	—	—	—	—	—	295
—	—	—	Summer	—	—	—	—	—	—	—	—	297
—	—	—	—	—	—	—	—	—	—	—	—	298

of the Forests

Mt. Moco (montane)		South-western (? montane)		Western (escarpment and riverine)				
8	Breeding	13	Breeding	15	18	20	Breeding	
—	—	—	—	1 ♂	—	—	—	1
1 ♂, 1 imm. ♂	? May/June	—	—	—	—	—	—	2
1 ♂	—	—	—	—	—	—	—	14
—	—	—	—	—	1 ♀	—	—	17
—	—	—	—	—	—	—	—	19
1 ♀	? Sept.	1 ♀	—	1 ♂	—	—	? Oct.	21
—	—	—	—	1	—	—	—	22
—	—	—	—	—	—	—	—	27
—	—	—	—	—	—	—	—	36
1 ♂	Summer	—	—	—	—	—	—	41
1 ♂, 1 ♀	? Sept.	—	—	—	—	—	—	43
—	—	—	—	—	1 ♀	—	? Aug.	44
1 ♀	—	—	—	1 ♂	—	—	? July	47
2 ♀	? Sept.	—	—	—	—	—	—	50
1 ♂, 1 ♀	—	—	—	—	—	—	—	53
—	—	—	—	—	—	—	—	55
—	—	—	—	—	—	—	—	58
—	—	—	—	—	1 ♂	—	Summer	60
1 ♂, 2 imm.	—	—	—	—	—	—	—	62
—	—	—	—	1 imm. ♂	—	—	July	63
3 ♂, 1 ♀	? Aug. onwards	—	—	—	—	—	—	83
—	—	—	—	—	3 ♂	—	? July	84
1 ♂	? July	—	—	—	—	—	—	86
—	—	—	—	—	1 ♂, 1 ♀	—	? July	87
—	—	—	—	—	—	—	—	88

TABLE II.—

	Other references		Eastern Districts (riverine)		
	Tables	Syst. Notes	1	2	Breeding
89 Chlorocichla f. falkensteini	—	*	—	—	—
90 flaviventris occidentalis	—	—	—	—	—
91 flavicollis flavigula	—	—	—	1 ♂	? June
92 Phyllastrephus fischeri cabanisi	—	—	—	1 ♂, 1 imm. 1 (2)	? May/June
93 fulviventris	—	*	—	—	—
95 Alseonax cassini	—	—	—	—	—
98 Chloropeta natalensis major	—	—	—	—	—
99 Parisoma plumbeum orientale	—	—	—	—	—
104 Dioptrornis brunneus bailundensis	—	—	—	—	—
109 Batis m. margaritae	—	*	—	—	—
110 minulla	—	—	—	—	—
111 Platysteira peltata mentalis	I	—	1 ♂	2 ♂	—
112 Dyaphorophyia concreta ansorgei	—	*	—	—	—
113 Elminia albicauda	I	—	—	—	—
114 Tchitrea viridis plumbeiceps	I	*	—	—	—
melampyra bannermani	—	*	—	—	—
117 Turdus olivaceus stormsi	—	—	1 ♂, 1 ♀	—	? Sept.
118 pelios bocagei	—	*	—	—	—
131 Cossypha heuglini heuglini	—	—	—	1 ♀ (1)	? June
subrufescens	—	—	—	—	—
132 polioptera polioptera	—	*	1 ♂, 2 ♀	—	—
133 natalensis intensa	—	*	1 ♂, 1 ♀	1 imm. ♀	? May/June
larischi	—	—	—	—	—
134 b. bocagei	—	—	—	—	—
135 Alethe p. poliocephala	—	—	—	—	—
136 Cichladusa ruficauda	—	—	—	—	—
139 Erythropygia leucosticta reichenowi	—	*	—	—	—
142 Seicercus laurae	—	*	—	—	—
143 Bradypterus mariae boultoni	—	*	—	—	—
149 Apalis rufogularis brauni	—	*	—	—	—
150 cinerea grandis	—	—	—	—	—
153 Sylvietta virens tando	—	—	—	—	—
159 Camaroptera brevicaudata sharpei (?)	I, IV	*	—	—	—
harterti	—	—	—	—	—
169 Cisticola erythrops lepe	—	—	—	—	—
178 Prinia l. leucopogon	—	—	1 ♂, 1 ♀	—	—
180 Hirundo abyssinica unitatis	—	*	—	—	—
193 Campephaga phoenicea sulphurata	—	—	—	—	—
194 q. quiscalina	—	—	—	—	—
196 Dicrurus l. ludwigii	—	—	—	—	—
199 Prionops gabela	IV	*	—	—	—
203 Lanius mackinnoni	—	—	—	—	—
208 Dryoscopus cubla hamatus	I, IV	—	—	—	—
209 a. angolensis	—	—	—	—	—
214 Chlorophoneus multicolor batesi	—	*	—	—	—
215 nigrifrons manningi	—	*	1 imm. ♂	—	? May/June
216 sulfureopectus similis	I	—	—	—	—
217 Telephorus viridis	—	*	—	—	—
219 Nicator vireo tando	—	—	—	—	—
229 Lamprotornis acuticaudus	I	—	—	—	—
231 Zosterops senegalensis quanzae ⋛ kasaica	I	*	—	—	—
234 Cinnyris superbus	—	—	—	—	—
236 bifasciatus	—	—	—	—	—
239 afer ludovicensis	I	—	—	—	—
244 Cyanomitra verticalis bannermani	—	—	—	1 ♂	? June
245 olivacea cephaelis	—	—	—	—	—
246 Anthreptes collaris somereni	I	*	—	—	—
phillipsi	I	—	1 ♂, 1 ♀	—	—
252 Passer griseus griseus	—	—	—	—	—
258 Ploceus x. xanthops	I	—	—	—	—
259 Symplectes bicolor kigomaensis	—	—	1 ♂	—	Summer
amaurocephalus	—	—	—	—	—
260 Hyphanturgus n. nigricollis	—	—	—	—	—
261 ocularis crocatus	—	—	1 imm. ♂	—	? May/June
270 Spermaphaga r. ruficapilla	—	—	—	—	—
271 Cryptospiza r. reichenovii	—	—	—	—	—
273 Hypargos niveoguttatus	—	—	1 ♂, 1 imm. ♂, 1 imm. ♀	—	? May/June
285 Estrilda p. perreini	—	—	—	1 ♀, 1 (1)	? June
288 Hypochaera nigerrima	—	—	—	—	—
296 Poliospiza burtoni tanganjicae	—	—	—	—	—

Continued

Mt. Moco (montane)		South-western (? montane)		Western (escarpment and riverine)				
8	Breeding	13	Breeding	15	18	20	Breeding	
—	—	—	—	1 ♂	1 ♀, 1 imm. ♀	—	? June/July	89
—	—	—	—	1 ♂, 1 ♀ 1 imm. ♀	—	—	—	90
1 ♂	? June	—	—	—	—	—	—	91
3 ♂, 2 ♀	Summer	—	—	—	—	—	—	92
—	—	—	—	1 ♂, 1♀, 1	1 ♂, 1 ♀	—	? Aug.	93
—	—	—	—	—	1 ♀	—	? Sept.	95
1	—	—	—	—	—	—	—	98
—	—	—	—	1 ♂	—	—	? Oct.	99
3 ♂, 2 ♀	? Sept.	—	—	—	—	—	—	104
2 ♂, 1 ♀	? July onwards	—	—	—	—	—	—	109
—	—	—	—	1 ♂, 2 ♀	1 ♂, 1 ♀	—	? Aug.	110
2 ♂, 2 ♀	—	—	—	—	—	1 ♀	? Oct.	111
—	—	—	—	3 ♂, 3 ♀, 1 juv. ♂	1 ♂, 1 ♀	—	? July	112
1 ♂	—	—	—	—	—	1 ♀	? July	113
1 ♂, 1 ♀	? Sept.	—	—	—	—	—	—	114
—	—	—	—	—	1 ♀	—	? July	
—	—	—	—	—	—	—	—	117
1 ♂	? Sept.	—	—	—	—	—	—	118
—	—	—	—	—	—	—	—	131
1 ♂	? Oct.	1 ♂, 1 ♀	—	1 ♀	—	—	Summer	
—	—	—	—	—	—	—	—	132
—	—	—	—	—	—	—	—	133
—	—	—	—	—	1 ♂, 2 ♀, 1 imm. ♀	—	July	
6 ♂, 2 ♀	Summer	1 ♀	Summer	—	—	—	—	134
—	—	—	—	—	1 juv. ♂	—	Aug.	135
—	—	—	—	1 ♂, 3 ♀	—	—	Summer	136
—	—	—	—	1 imm. ♀	—	—	? June	139
2 ♂, 2 ♀, 2 (1)	August	—	—	—	—	—	—	142
1 ♂, 2 ♀	? Sept. onwards	—	—	—	—	—	—	143
—	—	—	—	—	1 ♂, 2 juv. ♀	—	Aug.	149
2 ♂, 2 ♀	? Sept.	—	—	—	—	—	—	150
—	—	—	—	—	1 ♂, 1 ♀	—	—	153
—	—	1 ♂	—	1 ♂, 1 juv.	—	—	Aug.	159
—	—	—	—	—	1 ♀	—	? July	
1 ♂, 3 ♀	Summer	—	—	1 ♀	—	—	? July	169
—	—	—	—	—	—	—	—	178
1	? Aug.	—	—	—	—	—	—	180
—	—	—	—	—	1 ♀	—	? July	193
—	—	—	—	1 ♂	—	—	? July	194
—	—	—	—	1 ♂, 1 ♀	—	—	? Oct.	196
—	—	—	—	—	1 imm. ♀	—	? June/July	199
—	—	—	—	—	1 imm. ♂	—	? June/July	203
—	—	—	—	1 imm. ♀	2 ♂	—	? June/July, ? Oct.	20[illegible]
—	—	—	—	—	1 ♂, 1 ♀	—	? July	209
—	—	—	—	—	1 ♂, 1 imm. ♂	—	? June/July	214
—	—	—	—	—	—	—	—	215
—	—	—	—	1 imm. ♀, 1	—	—	? June/July	216
—	—	—	—	1 ♂, 1 ♀	—	—	—	217
—	—	—	—	—	1 ♀	—	? July	219
1 ♀, 1	—	—	—	—	—	—	—	229
—	—	—	—	—	1♀	—	? July	231
—	—	—	—	1 ♂	—	—	—	234
—	—	—	—	1 imm. ♂, 1 ♀	—	—	—	236
2 ♂, 2 ♀, 5 imm. ♂, 4 imm. ♀	? July	2 ♂, 1 ♀, 2 imm. ♂	? July	—	—	—	—	239
—	—	—	—	—	—	—	—	244
—	—	—	—	—	2 ♂, 1 imm. ♂	—	—	245
—	—	—	—	—	1 ♂, 1 ♀	—	—	246
—	—	—	—	—	—	—	—	
—	—	—	—	—	1 ♂	—	? July	252
—	—	2 ♂	—	—	1 ♀	—	—	258
—	—	—	—	—	—	—	—	259
—	—	—	—	2 ♀, 1 imm. ♂	1 ♀	—	? June/July	
—	—	—	—	—	2 imm. ♀	—	? June/July	260
1 ♂, 1 imm. ♂	June	—	—	—	—	—	—	261
—	—	—	—	—	1 ♂, 1 imm. ♀	—	? July	270
—	—	—	—	—	1 ♂, 1 ♀, 1 imm. ♂	—	July	271
—	—	—	—	—	—	—	—	273
—	—	—	—	1 ♀	—	—	? July	285
—	—	—	—	1 imm.	—	—	July	288
1 ♂, 2 ♀	? Sept.	—	—	—	—	—	—	296

TABLE III.—*Birds of Grasslands,*

		Other references		Eastern Districts				Central		
		Tables	Syst. Notes	1	2	3	Breeding	4	5	6
5	Francolinus levaillantoides jugularis	—	—	—	—	—	—	—	—	—
7	albogularis meinertzhageni	—	*	—	2 ♂, 3 ♀	—	Summer	—	—	—
8	Pternistes afer crainchii	IV	—	—	—	1 ♂	? June	—	—	—
10	Glareola pratincola fulleborni	—	—	—	—	1 ♀	Summer	—	—	—
12	Cursorius temminckii	—	—	—	—	—	—	1 juv. ♂	—	—
18	Centropus toulou grilli	—	—	—	—	—	—	—	—	—
26	Halcyon albiventris	—	—	—	1	—	—	—	—	—
38	Caprimulgus natalensis mpasa (?)	—	*	—	—	1 ♂	Summer	—	—	—
39	fossii	—	—	—	—	2 ♂, 2 ♀	Aug. onwards	—	—	—
42	Micropus caffer ansorgei	—	—	—	—	—	—	1 ♂	—	—
64	Mirafra africana occidentalis	—	*	—	—	—	—	—	—	—
	occidentalis ≷ pallida	—	—	—	—	—	—	—	—	—
	kabalii	—	—	—	2 ♂, 2 ♀	—	Summer	—	—	—
65	angolensis angolensis	—	*	—	—	—	—	1 ♀	3 ♂, 1 ♀	—
	antonii	—	—	—	6 ♂, 3 ♀	—	Summer	—	—	—
66	rufocinnamomea fischeri	—	—	—	1 ♀	—	—	1 ♂	—	—
69	Certhilauda albofasciata obscurata	—	—	—	—	—	—	—	3 ♂, 2 ♀	—
70	Calandrella cinerea saturatior	—	—	—	2 ♂, 2 ♀ 2 juv.	—	July	—	—	—
72	Eremopterix verticalis damarensis	IV	—	—	—	—	—	—	—	—
73	Motacilla capensis simplicissima	—	—	—	—	—	—	—	—	—
74	Anthus vaalensis neumanni	—	*	—	1 ♀	1 ♀	Summer	1 ♀	2 ♂, 1 ♀	1 ♀
75	leucophrys bohndorffi	—	*	—	—	—	—	—	—	—
78	Macronyx ameliae	—	*	—	1 ♂, 2 ♀, 1 imm. ♀	1 ♂	? July onwards	—	2 ♂	—
79	grimwoodi	—	*	—	1 ♂	—	? Oct.	—	2 ♂, 1 ♀	—
80	fulleborni ascensi	—	*	—	2 ♀	1 ♂	? Oct.	—	1 ♂, 1 ♀, 1	—
81	Turdoides leucopygia hartlaubii	IV	—	—	—	1 imm. ♀	? May/June	—	—	—
106	Hyliota flavigaster barbozae	I	—	—	—	—	—	—	—	—
122	Oenanthe pileata livingstonii (?)	—	—	—	—	—	—	—	1 ♂	—
126	Myrmecocichla nigra	—	—	—	1 ♂, 1 ♀	—	Summer	—	—	—
127	tholloni	—	*	—	—	—	—	—	2 ♂, 1 ♀	—
128	Saxicola torquata caffra		—	—	2 ♂	—	—	—	1 ♂, 1 ♀, eggs	—
141	Acrocephalus baeticatus cinnamomeus	—	*	—	—	—	—	—	—	—
145	Calamocichla gracilirostris winterbottomi	—	*	—	—	2 ♂, 2 ♀	? Sept.	—	—	—
	cunenensis	—	—	—	—	—	—	—	—	—
148	Schoenicola brevirostris alexinae	—	—	1 imm. ♀	—	—	—	—	—	—
160	Cisticola a. ayresii	—	—	—	—	—	—	—	—	—
161	lateralis vincenti	—	—	3 ♂, 2 ♀	—	—	Summer	—	—	—
162	natalensis katangae	—	—	(1)	—	2 ♀	Summer	—	—	—
	huambo	—	—	—	—	—	—	—	—	—
164	tinniens perpulla	—	—	—	1 ♂	1 ♂, 1 ♀	Summer	—	2 ♂	—
165	robusta angolensis	—	—	—	—	1 ♀	Summer	—	1 ♂	—
167	brachyptera loanda	—	—	1 ♀	—	1 ♂	Summer	1 ♂	—	—
168	pipiens congo	—	—	—	—	1 ♂	Summer	—	—	—
170	bulliens	—	—	—	—	—	—	—	—	—
171	emini bailundensis	—	—	—	—	—	—	—	—	—
172	lais namba	—	—	—	—	—	—	—	—	—
173	rufilata ansorgei	—	—	—	—	—	—	—	1 ♂	—
174	textrix mystica	—	—	—	—	—	—	1 ♂	—	—
	bulubulu	—	—	—	—	—	—	—	1 ♂, 1 ♀	—
175	aridula lobito	IV	—	—	—	—	—	—	—	—
176	dambo	—	—	—	2 ♂, 1 ♀ (2)	3 ♀ (1)	Summer	—	—	—
180	Melocichla mentalis grandis	—	—	—	—	—	—	—	—	—
182	Hirundo albigularis ambigua	—	—	—	—	—	—	1 ♂, 1 ♀	—	—
183	dimidiata marwitzi	—	—	—	—	—	—	—	—	—
184	senegalensis monteiri	—	—	—	—	—	—	1 ♂	—	—
185	s. semirufa	—	—	—	—	—	—	—	1 ♀	—
186	nigrorufa	—	—	—	—	1 ♂, 2 ♀	Summer	—	1 ♂	—
187	angolensis	—	—	—	—	—	—	—	—	—
188	griseopyga	—	—	—	(1)	—	—	—	—	—
189	Riparia c. cincta	—	—	—	—	—	—	—	—	—
190	Ptynoprogne fuligula rufigula	—	*	—	—	—	—	—	—	—
191	Petrochelidon rufigula	—	*	—	—	—	—	3 ♂, 6 ♀, (1) eggs	—	—
202	Lanius collaris capelli	—	—	—	1 ♂	—	—	—	—	—
257	Ploceus temporalis	—	*	—	—	—	—	1 ♂, 1	—	—
262	Euplectes orix orix (?)	—	—	—	2 ♀	—	? June	—	—	—
263	capensis zambesiensis	—	—	1	—	—	? June	—	—	—
	angolensis	—	—	—	—	—	—	—	—	—
265	Coliuspasser axillaris bocagei	—	—	—	—	2 ♂, 1 ♀, 2 imm. ♂	? May/June	—	—	—
266	h. hartlaubi	—	—	—	—	—	—	1 ♀	—	—
267	a. ardens	—	—	1 imm. ♂	—	—	June	—	—	—

Reeds and Open Country

Districts				Mt. Moco		South-western Districts				Western Districts				
7	9	20	Breeding	8	Breeding	10	11	13	Breeding	15	17	18	Breeding	
—	—	—	—	—	—	—	—	—	—		1 juv. ♀		Aug.	5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	7
—	—	—	—	—	—	—	—	—	—	—	—	—	—	8
—	—	—	—	—	—	—	—	—	—	—	—	—	—	10
—	—	—	July	—	—	—	—	—	—	—	—	—	—	12
—	—	—	—	—	—	—	—	—	—	—	1 ♀	—	? Oct.	18
—	—	—	—	—	—	—	—	1 ♂	—	—	—	—	—	26
—	—	—	—	—	—	—	—	—	—	—	—	—	—	38
—	—	—	—	—	—	—	—	—	—	—	—	—	—	39
—	—	—	—	—	—	—	—	—	—	—	—	—	—	42
—	—	—	—	—	—	—	1 ♂, 1 ♀	—	? Oct.	—	1 ♂, 1imm. ♂	—	July	64
—	—	—	—	—	—	—	—	1 ♂	? Oct.	—	—	—	—	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	
1 ♂	—	—	? Oct.	—	—	—	—	—	—	—	—	—	—	65
—	—	—	—	—	—	—	—	—	—	—	—	—	—	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	66
—	—	—	Summer	—	—	—	—	—	—	—	—	—	—	69
—	1 ♀	—	—	—	—	—	—	—	—	—	—	—	—	70
—	—	—	—	—	—	—	—	—	—	—	1 ♂	—	—	72
1 ♂, 1 ♀	—	—	—	—	—	—	—	—	—	—	—	—	—	73
—	—	—	Summer	—	—	—	—	1 ♂, 2 ♀	? Oct.	—	—	—	—	74
1 ♂	—	—	? Oct.	—	—	—	—	—	—	—	—	—	—	75
—	—	—	? Oct.	—	—	—	—	—	—	—	—	—	—	78
—	—	—	? Oct.	—	—	—	—	—	—	—	—	—	—	79
—	—	—	Summer	—	—	—	—	—	—	—	—	—	—	80
—	1 ♂	—	? July	—	—	—	—	—	—	—	—	—	—	81
—	—	—	—	1 ♀	? Sept.	—	—	—	—	—	—	—	—	106
—	—	—	? Sept.	—	—	—	—	—	—	—	—	—	—	122
—	—	—	—	—	—	1 ♂	—	—	—	—	—	—	—	126
—	—	—	? Sept.	—	—	—	—	—	—	—	—	—	—	127
—	—	—	Aug.	—	—	—	—	—	—	—	—	—	—	128
—	—	—	—	—	—	—	—	—	—	1 ♀	—	—	? July	141
—	—	—	—	—	—	—	—	—	—	—	—	—	—	145
—	—	—	—	—	—	—	—	1 ♀	? July	—	—	—	—	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	148
1 ♀	—	—	Summer	—	—	—	—	—	—	—	—	—	—	160
—	—	—	—	—	—	—	—	—	—	—	—	—	—	161
—	—	—	—	—	—	—	—	—	—	—	—	—	—	162
1 ♂, 2 ♀	—	—	Summer	—	—	—	—	—	—	—	—	—	—	
—	—	—	Summer	—	—	—	—	—	—	—	—	—	—	164
—	—	—	Summer	—	—	—	—	—	—	—	—	—	—	165
2 ♂, 1	—	1 ♂	Summer	1 ♀, 2	Summer	—	—	—	—	—	—	—	—	167
—	—	—	—	—	—	—	—	—	—	—	—	—	—	168
—	—	—	—	—	—	—	—	—	—	1 ♂, 2♀	1 imm.	1 ♂	July onwards	170
—	—	—	—	1 ♂, 2 ♀, 1	Summer	—	—	—	—	—	—	—	—	171
1 ♂ (1)	—	—	Summer	3 ♀	Summer	—	—	—	—	—	—	—	—	172
—	—	—	Summer	—	—	1 ♂	—	—	Summer	—	—	—	—	173
—	—	—	Summer	—	—	—	—	—	—	—	—	—	—	174
—	—	—	Summer	—	—	—	—	—	—	—	—	—	—	
—	—	—	—	—	—	—	—	—	—	—	1 ♂	—	Summer	175
—	—	—	—	—	—	—	—	—	—	—	—	—	—	176
1 ♂	—	—	—	—	—	—	—	—	—	—	—	—	—	180
—	—	—	? Sept.	—	—	—	—	—	—	—	—	—	—	182
—	1 ♀	—	? Sept.	—	—	—	—	—	—	—	—	—	—	183
—	—	—	? June	—	—	—	—	—	—	—	—	—	—	184
—	—	—	? Sept.	—	—	—	—	—	—	—	—	—	—	185
—	—	—	Summer	—	—	—	—	—	—	—	—	—	—	186
1 ♀	—	—	? Sept.	—	—	—	—	—	—	—	—	—	—	187
—	—	—	—	—	—	—	—	—	—	—	—	—	—	188
—	1	—	—	—	—	—	—	—	—	—	—	—	—	189
—	—	—	—	1	—	—	—	—	—	—	—	—	—	190
1 ♂, 2 ♀, 1	—	—	Aug.	—	—	—	—	—	—	—	—	—	—	191
1 ♂	—	—	—	—	—	—	—	—	—	—	—	—	—	202
—	—	—	? Sept.	—	—	—	—	—	—	—	—	—	—	257
—	—	—	—	—	—	—	—	—	—	—	—	—	—	262
—	—	—	—	—	—	—	—	—	—	—	—	—	—	263
—	1 ♂	—	? July	1	? July	—	—	—	—	—	—	—	—	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	265
—	—	—	—	—	—	—	—	—	—	—	—	—	—	266
1 ♀	—	—	? July	—	—	—	—	—	—	—	—	—	—	267

TABLE III.—

		Other references		Eastern Districts				Central		
		Tables	Syst. Notes	1	2	3	Breeding	4	5	6
268	Coliuspasser progne ansorgei	—	—	—	1 ♂, 1 ♀, 1 imm. ♂	—	? May/June	—	—	—
272	Ortygospiza atricollis minuscula	—	—	—	2 ♂ (1)	1 ♂	? June	—	—	—
275	Pytilia afra	—	—	—	—	—	—	—	—	—
277	Lagonosticta rubricata congica	—	—	1 ♀, 1 imm.	—	—	June	—	—	—
278	landanae	—	—	—	—	—	—	—	—	—
279	jamesoni ansorgei	—	—	—	—	—	—	—	—	—
280	nitidula	—	—	—	—	—	—	—	—	—
281	Clytospiza c. cinereovinacea	—	*	—	—	—	—	—	—	—
282	Coccopygia melanotis bocagei	—	—	—	—	—	—	—	—	—
283	Estrilda astrild niediecki	—	*	—	—	—	—	—	1 ♂	—
	angolensis	—	—	—	—	—	—	—	—	—
284	paludicola benguellensis	—	—	—	—	—	—	—	—	—
286	Uraeginthus bengalus katangae	—	—	1 ♀	—	—	? Sept.	—	—	—
290	Serinus mozambicus tando	—	—	—	—	—	—	1 ♀	—	—
292	flavivertex huillensis	—	—	—	—	—	—	—	—	—
293	atrogularis lwenarum	—	—	—	—	—	—	—	2 ♀	1 ♀

TABLE IV.—*Birds of the Thornbush, Semi-desert,*

		Other references			Thorn,
		Tables	Syst. Notes	11	12
3	Francolinus sephaena zambesiae	—	*	—	—
8	Pternistes a. afer	III	—	—	—
9	Numida mitrata (head only)	—	—	—	—
11	Rhinoptilus africanus bisignatus	—	—	—	—
13	Eremialector bicinctus ansorgei	—	—	—	—
20	Agapornis roseicollis catumbellae	—	—	—	—
23	Corythaixoides concolor pallidiceps	—	—	2 ♂	—
32	Tockus monteiri	—	—	—	—
33	Otus scops senegalensis	—	*	—	—
35	Bubo a. africanus	—	—	—	1 ♂
46	Colius indicus lacteifrons	—	—	—	—
47	castanotus	I, II	—	—	—
51	Tricholaema l. leucomelas	—	—	—	—
54	Pogonolius chrysoconus extoni	I	—	—	—
55	Indicator minor damarensis	II	*	—	—
58	Campethera abingoni annectens	—	—	—	—
61	Dendropicos fuscescens hartlaubii ≷ stresemanni	I	*	1 ♂, 1 ♀	—
67	Mirafra passerina	—	—	—	—
68	sabota ansorgei	—	—	—	—
71	Spizocorys starkii	—	—	—	—
72	Eremopterix verticalis damarensis	III	—	—	—
81	Turdoides leucopygia hartlaubii	III	—	1 ♀	—
85	Pycnonotus nigricans	—	—	—	—
96	Alseonax c. cinereus	—	*	—	—
100	Parisoma subcaeruleum ansorgei	—	—	—	—
101	Bradornis pallidus murinus	I	—	(1)	—
102	infuscata benguellensis	—	—	—	—
108	Batis pririt	—	*	—	—
120	Monticola brevipes kaokoensis	—	—	—	—
123	Oenanthe monticola albipileata	—	—	—	—
124	Cercomela familiaris angolensis	I	—	—	—
129	Karrucincla schlegelii benguellensis	—	—	—	—
130	Xenocopsychus ansorgei	—	*	—	1 ♂
138	Erythropygia leucophrys munda	—	—	1 ♀	—
	ovamboensis	—	—	—	—
140	paena benguellensis	—	—	—	—
144	Achaetops pycnopygius	—	—	—	—
146	Calamonastes fasciolatus pallidior	—	—	—	—
151	Apalis f. flavida	—	—	1 ♀	—
154	Sylvietta rufescens ansorgei	—	*	—	—
	mossamedes	—	—	—	—
155	Eremomela icteropygialis puellula	I	*	—	—
159	Camaroptera brevicaudata sharpei (?)	I, II	*	(2)	—

Continued

Districts				Mt. Moco		South-western Districts				Western Districts				
7	9	20	Breeding	8	Breeding	10	11	13	Breeding	15	17	18	Breeding	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	268
—	—	—	—	—	—	—	—	—	—	—	—	—	—	272
1 ♂	—	—	? July	—	—	—	—	—	—	—	—	—	—	275
—	—	—	—	—	—	—	—	—	—	—	—	—	—	277
—	—	—	—	—	—	—	—	—	—	—	—	1 ♂	? July	278
—	1	—	—	—	—	—	—	1 ♀	? July	—	—	—	—	279
—	1 ♀	—	? July	—	—	—	—	—	—	—	—	—	—	280
1 ♂, 1 ♀, 2 imm.	—	—	June	2 ♂, 2 imm.	June	—	—	—	—	—	—	—	—	281
2 ♂, 1 ♀ 2 imm.	—	—	June	2 ♀	? June	—	—	1 ♂	? June	—	—	—	—	282
—	—	—	? June	—	—	—	—	—	—	—	—	—	—	283
1 ♂, 1	—	—	—	—	—	—	—	—	—	—	—	—	—	
1 ♂, 1 ♀	—	—	? June	—	—	—	—	—	—	—	—	—	—	284
—	—	—	—	—	—	—	—	—	—	—	—	—	—	286
2 ♂, 1 ♀	—	—	? June	—	—	—	—	—	—	—	—	—	—	290
—	—	—	—	1 ♀	? Sept.	—	—	—	—	—	—	—	—	292
—	—	—	—	—	—	—	—	—	—	—	—	—	—	293

Tangled Thickets and Rocks of Western Districts

Thickets and Rocks						Semidesert		
13	15	17	19	Breeding	14	16	Breeding	
1 ♀	—	—	—	Summer	—	—	—	3
1 ♂, 2 ♀, 1 juv. ♀	—	—	—	July/Aug.	—	—	—	8
—	—	—	—	—	1 imm.	—	—	9
—	—	—	—	—	—	1 ♂	? July	11
—	—	—	—	—	1 ♂	—	? Oct.	13
1♀, 2 imm. ♂ 1 imm. ♀ (1)	—	—	—	—	—	—	—	20
—	—	—	—	Summer	—	—	—	23
—	—	—	—	—	1	—	? July	32
—	—	1 ♂	—	Summer	—	—	—	33
—	—	—	—	Summer	—	—	—	35
1 ♂	—	—	—	? July	—	—	—	46
—	—	1 ♂	—	? July	—	—	—	47
—	—	—	—	—	—	1 ♀	Summer	51
1 ♂	—	—	—	? Oct.	—	—	—	54
1 ♀	—	—	—	? July	—	—	—	55
—	—	1 ♂	—	Summer	—	—	—	58
—	—	—	—	? Oct.	—	—	—	61
—	—	—	—	—	1 ♂	—	? July	67
—	—	—	—	—	—	1 ♂, 2 ♀, 1	? July	68
—	—	—	—	—	—	2 ♀, 1	? July	71
—	—	—	—	—	—	1 ♂	—	72
1	—	—	—	Summer	—	—	—	81
2 ♀	—	—	—	? July	—	—	—	85
—	—	—	1 imm. ♀	July	—	—	—	96
—	—	—	—	—	—	2 ♂	? Aug.	100
1 ♂	—	—	—	? July	—	—	—	101
—	—	—	—	—	—	1 ♂, 1	? July	102
—	—	—	—	—	1 ♂	1 ♂, 2 ♀	? July	108
2♂, 2♀ 1 imm.	—	—	—	? May/June	1 ♂	—	? Oct.	120
—	—	—	—	—	—	1 ♂	—	123
—	—	—	—	—	1 ♀	1 ♂	—	124
—	—	—	—	—	—	1 ♀	? July	129
1 ♂, 1 ♀, 1	—	—	—	? Oct.	—	—	—	130
—	—	—	—	? Oct.	—	—	—	138
—	—	1 ♀	—	—	1 ♀	—	—	
—	—	—	—	—	—	1 ♂	? July	140
2 ♂	—	—	—	? Oct.	—	—	—	144
—	—	—	—	—	—	1 ♂	? July	146
2 ♀	1 imm.	—	—	July	—	—	—	151
—	—	—	—	—	—	1 ♂, 1 ♀	Summer	154
1	—	—	—	—	—	—	—	
—	—	—	—	—	1 ♀	1 ♂	Summer	155
—	—	—	—	—	—	—	—	159

TABLE IV.—

	Other references		Thorn,	
	Tables	Syst. Notes	11	12
162 Cisticola chiniana nr. frater	I	*	—	—
166 fulvicapilla hallae	I	—	—	1 ♀
175 aridula lobito	III	—	—	—
177 Prinia subflava ovampensis	I	—	1 ♀	—
179 flavicans ansorgei	I	—	—	—
199 Prionops gabela	II	*	—	—
206 Laniarius bicolor guttatus	—	*	—	—
207 atrococcineus	—	—	1 ♂, 1 ♀	—
208 Dryoscopus cubla hamatus	I, II	—	(1)	—
210 Lanioturdus torquatus	—	—	2 ♂, 2 ♀	—
212 Tchagra australis nr. damarensis	—	—	—	1 ♀
220 Parus afer benguelae	—	—	—	—
221 niger carpi	I	—	—	—
227 Lamprotornis n. nitens	—	—	—	1 ♂
228 mevesi mevesi	I	*	—	1 ♂
230 Onychognathus nabouroup benguellensis	—	—	—	—
241 Cinnyris fuscus	—	—	—	—
250 Plocepasser mahali ansorgei	—	—	—	—
251 Passer motitensis benguellensis	—	—	—	—
253 diffusus georgicus	—	—	—	—
255 Sporopipes squamifrons	—	—	—	—
256 Ploceus cucullatus collaris	—	—	—	—
264 Euplectes aurea	—	—	—	—
274 Pytilia m. melba	I	—	—	—
276 Lagonosticta senegala pallidicrissa	—	—	—	—
287 Granatina granatina	—	—	—	—
294 Poliospiza albogularis crocopygia	—	—	—	—
298 Enberiza f. flaviventris	I	—	1 ♀	—
299 Fringillaria capensis nebularum	—	—	—	—
300 t. tahapisi	—	—	—	—
301 i. impetuana	—	—	—	—

DISTRIBUTION THROUGHOUT AFRICA OF SPECIES FOUND IN ANGOLA

Woodland Birds (*Table I*)

The majority of birds collected in the Brachystegia woodlands belong to species, and even subspecies, with a wide distribution in tropical Africa. In some cases, as with the Groundscraper Thrush, *Geocichla litsipsirupa,* this extends from Abyssinia to South Africa ; in others, such as the warblers *Eremomela salvadorii* and *E. atricollis,* it is limited to the woodland areas of higher rainfall in Angola, south-western Belgian Congo and western Northern Rhodesia. Other species are limited to the drier woodland areas of southern Africa ; these include the shrike *Lanius souzae,* and the Angola Rock Thrush, *Monticola angolensis.*

Only three species listed exclusively in Table I have a more specialized distribution and all are highland birds. They are *Francolinus finschi* and the two sunbirds *Nectarinia bocagei* and *N. kilimensis* ; the francolin with a sporadic distribution in the highlands of Angola north to Brazzaville ; *N. bocagei* confined to the central highlands of Angola*, and *N. kilimensis* to the highlands of Angola and East Africa. There are also several well-differentiated subspecies endemic to the highlands of central Angola, the most distinct being the Angola race of the Brubru Shrike, *Nilaus afer affinis,* and of the seedeater, *Poliospiza gularis benguellensis.*

* Also at Kalandji, Kwango dist., Belgian Congo. (Schouteden, Rev. Zool. Bot. Afr. 59, 1959 : 326).

Continued

Thickets and Rocks						Semidesert		
13	15	17	19	Breeding	14	16	Breeding	
1 ♂	—	—	—	Summer	—	—	—	162
1 ♀	—	—	—	Summer	—	—	—	166
—	—	—	—	—	—	1 ♀	Summer	175
1 ♀	—	—	—	? July	—	—	—	177
—	—	—	—	—	1 ♂, 1 ♀	1 ♂, 1	? July	179
—	—	—	1 ♀	? July	—	—	—	199
1 ♂, 2 ♀, 1 imm. ♂	1 imm.	1 ♂	—	July/Aug.	—	—	—	206
—	—	—	—	—	—	—	—	207
1 ♀	—	—	—	? July	—	—	—	208
—	—	—	—	? Oct. onwards	—	—	—	210
—	—	—	—	Summer	—	—	—	212
—	—	—	—	—	—	1 ♂, 1 ♀	? July	220
1 ♂, 1 ♀	—	1 ♀	—	? July onwards	—	—	—	221
—	—	—	—	? July	1 ♀	—	—	227
—	—	—	—	Summer	1 ♂	—	Summer	228
—	—	1 ♀	—	Summer	—	—	—	230
—	—	—	—	—	—	3 ♂, 2 ♀, 1 imm.	? Oct. onwards	241
—	—	—	—	—	1 ♀	—	? July	250
—	—	—	—	—	—	1 ♂	? July	251
1 ♀	—	—	—	? July	—	—	—	253
—	—	—	—	—	—	1 juv.	Aug.	255
—	—	1 ♂, 1 ♀	—	? Oct.	—	—	—	256
—	—	—	—	—	—	1 ♂	? July	264
2 ♀	—	—	—	? July	—	—	—	274
1 ♂	—	—	—	? July	—	—	—	276
1 ♂	—	—	—	? July	—	—	—	287
—	—	—	—	—	—	1 ♂	? July	294
—	—	—	—	Summer	—	—	—	298
1 ♀	—	—	—	Summer	—	—	—	299
1 ♂, 1 imm. ♂, 1 imm. ♀	—	—	—	July	1 ♂	—	? July	300
—	—	—	—	—	—	2 imm. ♂	July	301

Eucalyptus plantations, common along the railway, have been included in this Table, but few birds were seen in them and the only ones noted as collected in them were the Paradise Flycatchers at Vouga.

Forest Birds (*Table II*)

The birds found in the eastern riverine forest have all a wide distribution in the lowland forests of tropical Africa. Many are found also in the riverine forests of northern Angola, outside the range of the expedition, but only three, the broadbill *Smithornis capensis*, the forest weaver *Symplectes bicolor*, and *Cossypha natalensis* were found as well at Chingoroi or Gabela, the last two represented by different subspecies. Two others, the greenbul *Phyllastrephus fischeri* and *Cossypha heuglini* were also in the montane forest on Mt. Moco.

Of the thirty species collected in the montane forest on Mt. Moco ten are not confined to forests; these include the Redbacked Coly, *Colius castanotus*, which has a limited distribution in western Angola, but the other nine have wide ranges. A further six species are widespread in both lowland and montane forest, *Tauraco corythaix*, *Chlorocichla flavicollis*, *Phyllastrephus fischeri*, *Turdus pelios*, *Cossypha heuglini* and *Cisticola erythrops*. Only the barbet *Gymnobucco calvus* is typically a species of the Guinea forests and is found also in lowland forest in Angola at Ndala Tando and Canzele. Three other species, *Batis margaritae*, *Seicercus laurae* and *Cossypha bocagei*, are found elsewhere only in patches of lowland evergreen forest of the southern Congo and the north of Northern Rhodesia, and the *Cossypha* also at Leba. Two species are limited to forest in Angola, *Francolinus swierstrai* from Mombolo, Hanha (the type of *Francolinus cruzi*, presumed forest), and Humpata (Rudebeck), and the flycatcher *Dioptrornis brunneus* only from Pungo Andongo and Humpata (Rudebeck), though this species is clearly closely allied to the montane species of East Africa, *D. fischeri* and *D. chocolatina*. The Greater Double-collared Sunbird, *Cinnyris afer*, has a unique distribution, being found, like the *Dioptrornis*, at Leba and Pungo Andongo, but also with other races on the highlands of Ruwenzori, the eastern Congo, Nyasaland and the lowland forest in South Africa. A Table is provided to show the distribution of the other seven species, all of which are confined to montane forest and are representatives of the relic montane fauna discussed by Chapin (1932 : 285) and Moreau (1952 : 888). The Angola population is subspecifically distinct in only four of these species in spite of the distance separating it from the nearest mountains in the Cameroons and Nyasaland.

Table of Distribution of Montane Forest Species

	Caprimulgus poliocephalus	*Heterotrogon vittatus*	*Viridibucco coryphaca*	*Pseudoalcippe abyssinicus* (including *atriceps*)	*Bradypterus mariae*	*Apalis cinerea* (excluding *alticola*)	*Poliospiza burtoni*
Moco and Mombolo	x	x	x	x	x	x	x
Fernando Po	—	x	—	y	—	x	—
Cameroon Mt.	—	x	y	y	y	y	y
Mts. of north Cameroons	—	x	y	y	y	y	y
Ruwenzori area	y	y	y	—	—	—	x
Mts. of Kivu and L. Edward	y	y	y	y	—	—	x
Mts. east of L. Tanganyika	—	—	—	x	—	—	x
Mts. of Abyssinia	y	—	—	y	—	—	—
Mts. of East Africa	y	y	—	y	y	y	y
Mts. of S. Sudan	—	—	—	y	—	—	—
Mts. of north Nyasaland	y	y	—	y	y	—	—
Mts. of south Nyasaland	—	y	—	y	y	—	—

x, same subspecies as on Mt. Moco. y, different subspecies from Mt. Moco.

The distribution of the birds found in the escarpment forest at Gabela and in the forest at Chingoroi emphasizes their northern association. Some, such as the shrikes *Chlorophoneus multicolor* and *Lanius mackinnoni* and the wattle-eye *Dyaphorophyia concreta*, range from West Africa along the northern edge of the Congo forest to East Africa, though with by no means a continuous distribution. The bluebill *Spermophaga ruficapilla* follows the southern edge of the forest to East Africa, while the akalat *Malacocincla fulvescens* and the greenbul *Andropadus latirostris* embrace both ranges. Two other greenbuls *Chlorocichla falkensteini* and *Phyllastrephus fulviventris*, the Red-crested Turaco, *T. erythrolophus*, and the bush-shrike

Telephorus viridis have limited ranges in the west from the Gulf of Guinea to their southern limits at Chingoroi. The Crimson-wing, *Cryptospiza reichenovii,* is found unexpectedly at Gabela rather than on Mt. Moco since it is a montane forest species in the Cameroons, Fernando Po, and in most of East Africa.

The most striking feature of the distribution of the Angola forest birds is the almost completely different avifauna of Mt. Moco and Gabela, the only species obtained by ourselves and/or Heinrich in both forests being the wide-ranging Tambourine Dove, *Turtur tympanistra,* the bush-shrike *Telephorus viridis,* and *Colius castonotus.* This is the more surprising in view of the small percentage of Moco birds that are elsewhere restricted to mountains, others being found in the northern forests of Pungo Andongo, Ndala Tando and Canzele where most of the Gabela species are also found. The two localities are only 120 miles apart and the one-time montane forests of Mombolo were even closer to Gabela. Since the montane forest is recognized as being older than the lowland forest of the Congo Basin (Moreau 1952 : 908) it suggests that the escarpment forests may also be of a relic type but have been more subject to invasion by lowland species from the north than the more isolated montane forest.

The distribution of the birds also points to interesting affinities between the forest remnants in the Leba and Humpata areas and the montane forest of Mt. Moco, and also between the montane forest and some forest patches of north-western Northern Rhodesia.

Grassland Birds (*Table III*)

The distribution of the grassland birds found in Luacano and Vouga is quite fascinating and, to me, inexplicable. Typical species of these grasslands are the three longclaws, *Macronyx ameliae, M. fülleborni* and *M. grimwoodi,* the widow *Coliuspasser progne,* and the Angola Lark, *Mirafra angolensis,* all found at both places ; the Spike-heeled Lark, *Certhilauda albofasciata,* though collected by us only at Vouga as been found also in the eastern districts near Vila Luso. Thollon's Chat, *Myrmecocichla tholloni,* was found at Vouga only, and *Francolinus albogularis* at Luacano only. All of these, when present in the area, were found within short distances of each other and would therefore be expected to have the same requirements and therefore similar ranges throughout Africa, yet each is completely different. Among the longclaws the yellow *M. fülleborni* is the local variant in Angola, Northern Rhodesia, and the southern Congo of the widespread *M. croceus* ; the redthroated *M. ameliae* is primarily an East African species spreading westwards through Northern Rhodesia to its western limit in central Angola ; the larger *M. grimwoodi* was known only from north-western Northern Rhodesia until we found it first on the road to Luacano and later as far west as Vouga.

The Angola Lark is confined to the highlands of central Angola. the grasslands of the Zambesi/Congo watershed and north-western Northern Rhodesia, and the Marungu highlands of the south-eastern Belgian Congo. The Spike-heeled Lark is essentially a bird of the dry western semi-desert areas of South West Africa, and the pans and grasslands of Bechuanaland and the Transvaal. It has recently been found by Rudebeck on the Humpata plateau and in the coastal strip north of Moçamedes.

The francolin is West African, known for a long time only from scattered localities in the hinterland from Senegal to Nigeria, but recently discovered on the Marungu highlands, eastern Belgian Congo and in the Balovale area of Northern Rhodesia.

Thollon's Chat is limited to the grasslands of the western plateaux of the French Congo and Angola, between the equator and 13° S.

The Long-Tailed Widow has a broken distribution, being found on the highveld grasslands of the Transvaal and neighbouring provinces, in a strip across central Africa from Lake Bangweola to central and southern Angola, and in the highland grasslands of Kenya.

From our own limited observations and from those of C. W. Benson (in litt.), and C. M. N. White (1958) in Northern Rhodesia it seems that even in very limited areas the grassland species are segregated to a large extent by preference for moister or drier conditions. Thus the Spike-heeled Lark, *C. albofasciata*, a species with a preference for sandy soil, short grass, and poor vegetation, was found at Vouga on the higher, and therefore well-drained, parts of the undulating grasslands east of the village. It may be this factor of drainage which enables these larks to tolerate here an unusually high rainfall, over 40 inches a year, whereas in most of their range the rainfall is under 10 inches a year. Similarly, lack of good drainage on some of the flatter grasslands of the eastern districts would account for their absence there.

M. angolensis seems to require rather moister conditions than the Spike-heeled Lark, being collected at Vouga on the edges of the marshy valleys and by White at Balovale on the midslopes of the Minyanya plain. At Minyanya the ecological place of the Spike-heeled Lark on the upper slopes is filled by *M. africana*, which was found alongside *M. angolensis* at Luacano, where the limited amount of grassland in the surrounding districts and the uniform flatness of the plains may have brought the species together through lack of their preferred habitats.

The francolin, longclaws and widow-bird were associated with the dampest areas of the grasslands. The widows were in flocks along the ditches at Luacano, though in north-eastern Northern Rhodesia Benson found them associated with *M. africana* on the drier grasslands. All the longclaws were collected in similar conditions in very rank grass and in the marshy valleys. They seemed in Angola to be competitive species since all had been feeding on grasshoppers and beetles : Benson, however, found that the yellow species *fulleborni* and *croceus* in Rhodesia prefer drier parts than do the red-throated species, *M. ameliae* and *M. grimwoodi*. It may be that the widespread yellow species are more adaptive to differing conditions than the red-throated species, especially *M. grimwoodi*.

Some of the francolins were found to have been eating frogs and fish, the latter possibly among those that had been left stranded with the drying up of the summer floods. It is most improbable that fish or frogs form an essential part of the diet of *F. albogularis* (others collected by Serle in Nigeria had been feeding on cassava), but high rainfall does seem to be a primary requirement for the species since the range lies entirely in the area between the 40-inch and 60-inch isohyets.

It is easy to see therefore, why all the species of the wetter parts of the grassland should be absent from the dry grasslands of south-western Africa, but not apparent why each should have such differing ranges within the wetter areas, the broken distribution of *Coliuspasser progne* being particularly surprising.

From our observations of Thollon's Chat it would seem unlikely to be found except where there are occasional small trees or bushes on which to perch, these perches being used as observation posts to which the birds returned time and again after foraging. Lack of suitable perches would account for their absence on the Luacano plains, and if all the grasslands of the eastern districts are similar to those we crossed, this may be the limiting factor in distribution of the species eastwards.

Among other families classed in Table III are many cisticolas and members of the Finch family that are birds of grasses and reeds rather than open grassland. Most of these are wide-spread but many of them have local and very distinctive races in central and western Angola.

Birds of the Western Thornbush, Semi-desert, Rocks and Tangled Thickets (*Table IV*)

In contrast to the complexities of distribution among the grassland birds of the central and western districts the ranges of all western species follow regular and comprehensible lines governed by the topography of south-western Africa and the limits of the thornveld. Thus, with the exception of *Euplectes aurea* which was possibly introduced from São Tomé, all the species collected in the semi-desert areas are found in similar areas in South West Africa, though in many cases are racially distinct.

Typical thornveld species such as the Pied Barbet, *Tricholaema leucomelas*, and the gregarious larks such as *Eremopterix verticalis*, have a wider distribution through the Kalahari and have been found, or can be expected, in Angola as far north as Luanda (see Serle, 1955), while species more typical of the Vornamib scrub such as Schlegel's Chat, *Karrucincla schlegeli*, are unlikely to be found north of Lobito.

Similarly, among the rocks of the Chela escarpment are such species as the Pale-winged Starling, *Onychognathus nabouroup*, the rock-jumper, *Achaetops pycnopygius*, and the Chat-flycatcher, *Laniotturdus torquatus*, all of which have limited ranges in the highlands of south-western Africa. The range of the indigenous *Xenocopsychus ansorgei* is even more limited, being apparently restricted to the rocks of the Chela escarpment and in the neighbourhood of Mt. Moco.

The overall pattern is of the predominantly South West African avifauna petering out northwards along the coast and the edge of the escarpment.

AVIFAUNAL ZONES AND SPECIATION

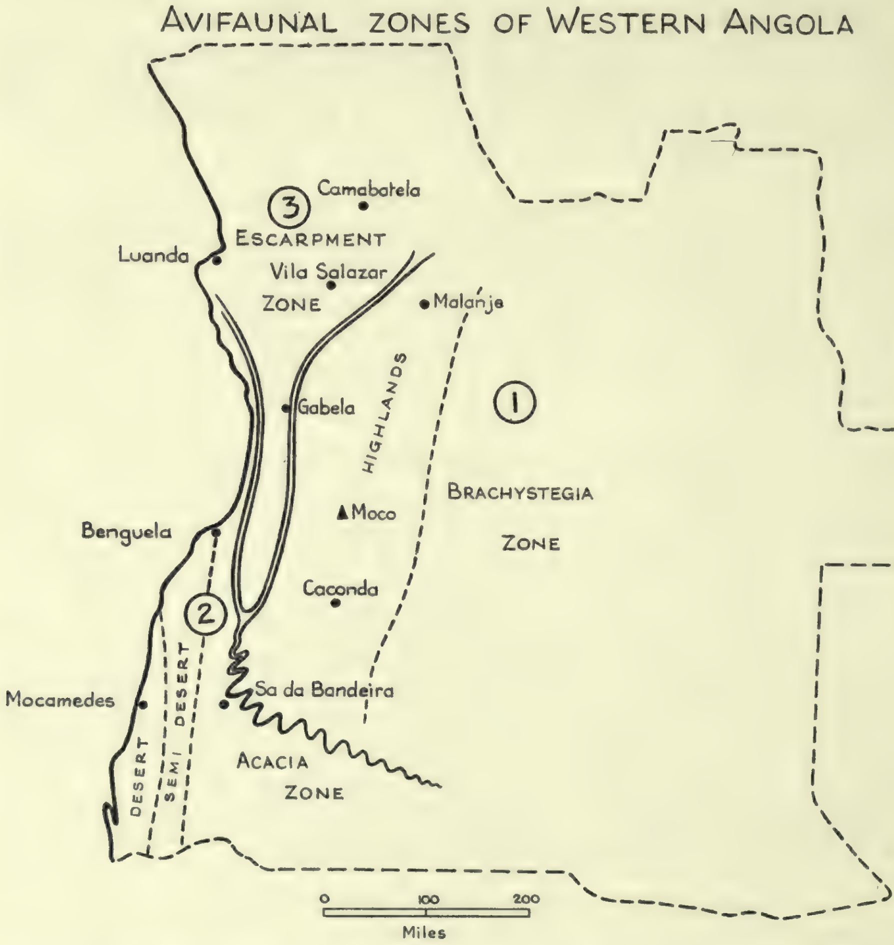
Avifaunal Zones

The distribution of birds found in the different types of vegetation has been discussed at some length because it seems that an understanding of this factor is primarily important in assessing the relationship between many forms found in Angola. Repeatedly it will be found that birds of many different families have similar specific or sub-specific ranges which lie along the same boundaries and coincide with the limits of one or another type of vegetation.

Thus western Angola can be divided into three avifaunal zones (see Map) :—

Zone 1. Above the escarpment and coinciding with the limits of Brachystegia woodland from the Sá da Bandeira area north at least to Malanje. This I shall call the Brachystegia Zone and in it East and Central African species and subspecies predominate.

Zone 2. The Acacia Zone, including the desert and semi-desert and poorer parts of the coastal plain, and the thorn country on top of the escarpment south and west of the Brachystegia Zone. In this South West African species and subspecies predominate.


AVIFAUNAL ZONES OF WESTERN ANGOLA
③
Camabatela
ESCARPMENT
Luanda
Vila Salazar
ZONE
Malanje
HIGHLANDS
①
Gabela
BRACHYSTEGIA
ZONE
Moco
Benguela
Caconda
②
SEMI DESERT
Mocamedes
Sa da Bandeira
DESERT
SEMI DESERT
ACACIA
ZONE
0
100
200
Miles

Zone 3. The north-western coastal lowlands where a richer and more varied vegetation is found than in Zone 2, and the escarpment area including the escarpment forests. This I shall call the Escarpment Zone. Little collecting was done in it except in the forests at Chingoroi and Gabela and therefore the distribution of birds, other than forest species, has not been discussed ; it would seem however to contain a number of interesting endemic forms about which much remains to be learnt. These include the two newly-discovered species *Prionops gabela* and *Muscicapa gabela,* both found originally in secondary forest and the *Prionops* since found in thickets below the escarpment : also the warbler, *Macrosphenus pulitzeri,* known only from the type specimen, and the forest greenbuls, *Chlorocichla falkensteini* and *Phyllastrephus fulviventris*. Among endemic forms are three which have been discussed in the Systematic Notes, *Malaconotus hypopyrrhus blanchoti*, *Camaroptera brevicaudata harterti* and *Tchitrea melampyra bannermani*.

The Escarpment Zone may even be found to extend in pockets as far south as Vila Arriaga and Capangombe as has been suggested in the Systematic Notes in the discussion on the distribution of the two races of *Lamprocolius mevesii*.

The interest of these zones lies in the fact that the zonal limitations are applicable to some birds that are not primarily associated with the typical vegetation ; for example *Cercomela familiaris* is a bird of rocks and kopjes rather than woodland or thornbush, but the two races *falkensteini* and *angolensis* are confined respectively to the Brachystegia and Acacia Zones. Similarly, the Black Tit, *Parus leucomelas insignis*, is found only outside woodlands in clearings or thickets but its true range is limited to Brachystegia Zone with an atypical population in the Escarpment Zone but not probably in the forest. It should, in fact, be emphasized that the zonal limits of the Escarpment Zone probably apply less to typical forest birds than to others, for several forest species are found in patches of riverine forest and in montane forest, within the Brachystegia Zone.

On the Map the zig-zag line dividing Zones 1 and 2 is intended to indicate that the two zones interlock where patches of Acacia and Brachystegia alternate. Some sub-divisions of Zones 1 and 2 have been shown, which were indicated in the discussion on distribution. No attempt has been made to define the zonal limits in the northern and south-eastern parts of the country from which little or no information on the birds is available.

Speciation

The rapid changes of vegetation and of altitude in the west of the country which are responsible for forming the zonal boundaries and the pockets of forest, allow closely related forms associated with specialized habitats to live in proximity without interbreeding. These forms can either be closely allied species or subspecies. A typical example of representation by species is found in the Batis flycatchers, in which *B. molitor* is the representative in the Brachystegia Zone, *B. pririt* in the Acacia Zone, *B. minulla* in the Escarpment Zone and possibly also in riverine forest in the north, and *B. margaritae* in montane forest, while the two races of shrike, *Lanius collaris capelli* and *L. c. subcoronatus* provide examples of subspecies in the Brachystegia and Acacia Zones which do not apparently intergrade.

Between good species like those of the genus Batis and subspecies like the shrikes there are other couplets or triplets of zonal representatives or forms ecologically separated whose relationship cannot confidently be defined. It would seem that through segregation they are in the process of developing into good species and are at varying stages in the process.

In recent studies on various African birds the problem has been discussed of forms which behave as good species in one part of their range and as subspecies elsewhere, by authors such as Chapin, Moreau, Benson, White and Stuart Irwin. It will be found that for most of the birds considered western Angola is a critical area in which speciation seems more advanced than in other parts of Africa, and it is hoped to develop this conception more fully in a later paper. Meanwhile the following list attempts to place in order some Angolan pairs or groups according to their degree of speciation, with the examples heading the list of forms that are no more than well-differentiated subspecies, grading through those of more doubtful relationship to some that behave as true species at the end of the list. Some of these pairs are zonal representatives, for the others there is some other ecological factor causing segregation which is indicated if possible. Reference is also made to papers in which the relationship has been discussed.

The conventions of trinomial nomenclature compel one to make a dividing line between pairs considered subspecies and pairs considered species, although for forms in the centre of the list there are arguments for and against either treatment ; it seems impossible to attain consistency since each problem is different and is aggravated by lack of data on such characters as voice, behaviour, nest and eggs. Far more also will be known about the relationship between some of the pairs in the Brachystegia and Acacia Zones when adequate collecting has been done along their boundary in the south and south-eastern districts of Angola.

Only in one example quoted, the Spur-fowl, *Pternistes afer*, does it seem possible that the process of speciation has been reversed and that, instead of forms evolving differences through isolation in different habitats, two very dissimilar forms *afer* and *crainchii*, which once may have appeared good species, have come together and hybridized and must now be considered conspecific. This suggestion of hybridization is put forward tentatively since this is the only case in western Angola in which intermediate populations are found, not apparently associated with vegetational changes, linking two highly differentiated forms of the thorn and Brachystegia country. Furthermore, these intermediate populations (to which the names *benguellensis* Bocage, *chio* Meise, and *cambatelae* Meise, have been given) show a degree of individual variation more commonly associated with hybrid populations than with populations of an established species.

Examples of Stages of Speciation

Erythropygia leucophrys manda (bushes in Zone 1) *Erythropygia l. ovambensis* (bushes in Zone 2)	Subspecies showing intergradation.
Prodotiscus i. insignis (Zone 3, forest ?) *Prodotiscus i. lathburyi* (Zone 1, highlands) *Prodotiscus i. zambesiae* (elsewhere)	*P. i. lathburyi* a subspecific link between, *insignis* and *zambesiae.*
Zosterops senegalensis quanzae (highland in Zone 1) *Zosterops s. anderssoni* (Zone 2) *Zosterops s. heinrichi* (Zone 3)	Subspecies showing intergradation. See Moreau, 1957, and Systematic Notes.

Pternistes afer afer (Zone 2) *Pternistes afer crainchi* (Zone 1)	Well-marked forms linked through hybrid populations. See above, and Bowen, 1930.
Prinia flavicans bihe (bushes on Vouga grasslands, Zone 1) *Prinia f. ansorgei* (thornbush, Zone 2)	Probably well-defined subspecies, isolated from each other. See Irwin, 1959.
Mirafra africana occidentalis (grasslands of Zones 2 and 3) *Mirafra a. kabalii* (grasslands of eastern Zone 1)	Well-differentiated forms probably subspecies : widely separated geographically. See Systematic Notes.
Nilaus afer affinis (highland Brachystegia, Zone 1) *Nilaus a. brubru* (thornbush, Zone 2)	Well-differentiated forms often considered species but with some intergrades recorded.
Laniarius luhderi amboinensis (escarpment forest ?, Gabela, Zone 3) *Laniarius l. brauni* (escarpment forest, Quicolungo, Zone 3)	Exceptionally well-differentiated forms about which little is known.
Eremomela icteropygialis polioxantha (woodland in Zone 1) *Eremomela i. puellula* (thornbush in Zone 2) *Eremomela salvadorii* (woodland Zone 1)	The first two well-defined subspecies ; *salvadorii* probably a closely related species overlapping in range. See Systematic Notes.
Lanius collaris capelli (bushes in Zones 1 and 3) *Lanius c. subcoronatus* (bushes in Zone 2)	Well-defined forms with close ranges but no recorded intergradation.
Malaconotus hypopyrrhus monteiri (Zone 3) *Malaconotus h. interpositus* (bushes, Zone 1)	Well-defined forms with close ranges but no recorded integradation. See Systematic Notes.
Lamprotornis mevesii mevesii (mopane belt, Zone 2) *Lamprotornis m. benguelensis* (southern tip of Zone 3)	Well-defined forms living in very close proximity ; no apparent intergradation. See Systematic Notes.
Cercomela familiaris falkensteini (rocky hills in Zone 1) *Cercomela f. angolensis* (kopjes in Zone 2)	Well-defined forms living in very close proximity; no known intergradation.
Camaroptera brevicaudata harterti (forest undergrowth, central Zone 3) *Camaroptera b. sharpei* (undergrowth, Zone 2 and southern Zone 3) *Camaroptera brevicaudata* near *sharpei* (undergrowth, Zone 1) *Camaroptera b. tincta* (undergrowth, northern Zone 2)	*harterti* possibly a species. See Systematic Notes.

Tchitrea melampyra bannermani (forest, Zone 3) *Tchitrea viridis plumbeiceps* Zones 1 and 2, also 3 outside forests)	Possibly hybrid populations originally, now re-established as sympatric species. See Systematic Notes.
Passer griseus griseus (habitations—widespread) *Passer diffusus diffusus* (away from habitations, Zones 2 and 3)	Well-differentiated forms with possibly overlapping ranges. See White & Moreau, 1958, and Benson, 1956.
Lagonosticta landanae (Zone 3 and western Zone 1) *Lagonosticta rubricata congica* (eastern Zone 1)	Well-differentiated forms with close ranges in Lower Congo: considered conspecific by Chapin.
Parus niger carpi (Zone 3 outside desert and semi-desert) *Parus leucomelas insignis* (typical) (Edges of woodland, Zone 1) *Parus leucomelas insignis* (atypical) (Zone 3)	*carpi* a well-differentiated form living in close proximity to *P. leucomelas*. See Hall, 1959.
Parus griseiventris (woodlands in Zone 1) *Parus afer benguelae* (semi-desert, Zone 2)	*griseiventris*, probably good species known to overlap elsewhere with *P. afer*, but possibly isolated from it in Angola by the Mopane belt. See Hall and Traylor, 1959, and Irwin, 1959.
Laniarius aethiopicus major (undergrowth in woodlands, Zone 1) *Laniarius bicolor guttatus* and *sticturus* (undergrowth, reeds etc. in Zones 2 and 3)	Probably good species known to overlap elsewhere through geological segregation, living in close proximity in Angola. See Hall, 1954.
Pycnonotus nigricans (Zone 2) *Pycnonotus barbatus* (Zone 1)	Apparently good species but with possible hybridization in western Angola. See Irwin, 1958.
Elminia albicauda (woodlands and forest, Zone 1) *Elminia longicauda loandae* (forests, Zone 3)	Species living in close proximity on the zonal boundary.
Prionops gabela (forest and thickets, Zone 3) *Prionops retzii* (elsewhere)	Closely allied species, but with little data on their relationship.
Turdus libonyanus verreauxi (woodland and bush) *Turdus pelios bocagei* (forests of west) *Turdus olivaceus stormsi* (forests of east)	*T. libonyanus* a good species ecologically segregated from the others which are possibly conspecific.
Monticola angolensis (woodland and bushes, Zone 1) *Monticola brevipes* (rocky terrain, Zone 2)	Good species, closely related, representative of each other in their respective Zones.

BREEDING SEASONS IN ANGOLA

General Discussion

From a collection such as this, taken only during the months of August and September and with a limited number of specimens of each species, generalizations on the regular breeding seasons must necessarily be limited ; nevertheless some useful data are provided by the presence of young birds and by the condition of the gonads and plumage, as to the probable breeding months of individual birds. In the Tables of Specimens Collected an estimate of the approximate breeding month has been made in all cases in which there appears to be sufficient evidence to warrant it. Nest with eggs, and young birds not fully grown, provide the only incontrovertible evidence—these young birds are listed in the Tables as " juvenile ;" young birds, fully grown, are classified as " immature." Some of these immature birds, still with considerable amounts of young plumage, also give some certainty within one or two months, especially when they are supported by adults in post-breeding moult. The estimated breeding month of these, as with juveniles and eggs, is put without a query in the Tables. The date of breeding of older, but still not fully adult passerines, is far more uncertain and has been indicated vaguely as ? May/June or ? June/July to show that it probably took place at the ends of the rains (see Table of Rainfall) or the beginning of the dry season rather than in the early or middle part of the rainy season.

Specimens in which the skull is not fully ossified are also classed as " immature ", but my knowledge of the length of time that full ossification takes in different families is too limited to allow me to make an estimate of breeding season on this evidence alone. Among sunbirds in particular a high proportion of apparently adult birds were noted as having ossification incomplete.

The condition of gonads and plumage has also been considered in conjunction, though it is appreciated that both can be misleading in birds of the tropics. Those specimens in worn plumage with active gonads have been considered as possible breeders in the month or two months following collection, i.e. in the early rains ; those in very fresh plumage, or post-breeding moult, showing no breeding activity, as possible breeders two months prior to collection, and therefore during the dry season or winter ; those with non-active gonads, in indeterminate plumage, non-breeding dress, or moulting from non-breeding dress have been classified as " summer " breeders on the assumption that they had not bred recently and are unlikely to do so before November.

On these estimates it is possible to make some cautious contributions to the tables of breeding activity in Africa published by Moreau (1950). It would be expected that Angola would fall into the regular pattern of the countries of southern Africa which have summer rainfall. In these countries, which include the Rhodesias, Nyasaland, and northern parts of the Union, the peak of breeding activity is found in September to December, that is in the early months of the rains and the two months preceding the rains, while in the dry winter months of May to August there is very little breeding activity except amongst birds of prey. In South West Africa, also an area of summer, but erratic, rains Macdonald (1957 : 30) found a progressive retardation of the breeding season from south to north with evidence that birds of Damaraland and the Kaokoveld have a peak activity from December to March.

It was therefore unexpected to find evidence of considerable breeding activity in Angola in the dry winter months of June to August. Young birds of over fifty species were collected in August and September. These were found in all the main vegetational regions and were of widely assorted families. In addition nest and eggs were found in August of the Stone Chat, *Saxicola torquata,* and the martin *Petrochelidon rufigula.* Some rainfall figures relevant to the discussion are included in the Tables on p. 403 :—

Non-passerines

Comparatively few non-passerines were collected and these for the most part indicated the expected summer breeding seasons in all species in the eastern and central districts whether woodland, forest, or grassland, except for a juvenile *Cursorius temminckii* collected west of Munhango on 12th August, and a juvenile *Colius castanotus* on Mt. Moco. In the western districts, in the semi-desert areas, the courser, hornbill and coly were in post-breeding moult : in the grasslands and evergreen thickets juveniles were obtained of *Pternistes afer,* and *Francolinus levaillantoides.*

The passerines are best discussed by ecological groups and districts according to the Tables.

Passerines of the Savannah Woodlands (Table I)

The flycatchers, thrushes and warblers generally indicate an August/September or a " summer " breeding season, sometimes slightly in advance of the corresponding families in Rhodesia, but similar to them in relation to the onset of the rains which start a little earlier in Angola. The shrikes and finch family appear irregular with some dry-season activity. The sunbirds, as in Northern Rhodesia and the southern Congo, seem frequently dry-season breeders.

Passerines of the Forests (Table II)

In the eastern riverine forests a number of indications of early winter or late summer breeding is provided by immature but nearly fully adult specimens, with rare indications of spring or early summer activity. On Mt. Moco, on the contrary, most birds had active gonads in August, and the Striped Swallow, *Hirundo abyssinica,* and *Seicercus laurae* were observed apparently engaged in nesting activities. The only winter breeder was apparently the weaver *Hyphanturgus ocularis.*

In the western forests the indications were of a peak season in June/July, very few species collected not being represented by either a juvenile or immature specimen; many of the latter among the thrushes and finches were still largely in first plumage although the shrikes and bulbuls were apparently older, the indications of immaturity being in the bill colour, skull ossification, or in a few remaining immature feathers. It would therefore seem that in these patches of forest the birds of the trees and forest canopy have a breeding season slightly in advance of the birds of the under-

Some Rainfall Figures Relevant to the Discussion Measured in Inches, Less Than One Tenth of an Inch Shown as Trace " tr "

Rainfall in 1957 (Localities on the Expedition Route)

Locality	Years	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.	Year's total
Texeira de Sousa	1957	10·2	5·9	9·6	0·3	?	—	—	?	2·1	4·8	3·6	8·3	44·8 plus
Nova Lisboa	1957	6·5	5·9	6·7	2·8	tr.	—	tr.	tr.	2·0	2·6	9·2	13·1	48·8
Sâ da Bandeira	1957	3·5	4·1	12·6	5·2	—	—	—	—	0·4	8·7	6·2	8·0	48·7
Lobito	1957	tr.	0·9	11·6	7·4	—	tr.	—	—	0·3	0·4	2·8	1·4	24·8
Gabela*	1957	1·5	5·3	11·8	5·5	—	—	—	—	0·4	2·9	4·8	5·4	37·6
Quimberima	1957	First spring rains fell 27th September.												
Mt. Moco		No figures available : first spring rains fell very locally on 24th August.												

Monthly Averages in Eastern Angola and North-western Northern Rhodesia

Locality	Years	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.	Yearly average
Texeira de Sousa, 3,609 feet	1942–53	8·8	8·6	9·3	5·2	0·5	—	tr.	0·3	0·7	3·1	7·9	8·4	52·8
Mwinilunga, 4,447 feet	1921–55	8·9	8·0	8·1	3·3	0·3	0·1	tr.	tr.	0·6	3·7	7·5	9·5	50·0
Balovale, 3,577 feet	1920–55	8·5	6·9	5·8	1·2	tr.	—	—	tr.	0·3	2·3	4·4	8·9	38·3

Monthly Averages in Central Angola

Locality	Years	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.	Yearly average
Nova Lisboa, 5,577 feet	1940–54	8·7	7·8	9·8	5·7	0·4	—	tr.	tr.	0·6	5·5	9·6	8·9	57·0
Ganda, 4,790 feet, 55 m. N.E. of Chingoroi	1924–52	7·0	7·1	10·9	6·1	5·4	—	—	tr.	1·1	6·0	9·3	8·7	61·8
Gabela,* 3,586 feet	1947–55	2·9	4·6	6·8	10·2	1·4	—	—	tr.	0·3	2·0	5·0	3·4	36·6
Quimberima, 3,700 feet	1954–57 (Aug.)	4·4	1·1	7·7	8·5	0·8	—	—	—	1·4	5·5	10·0	5·8	45·2

Monthly Averages in South-western Angola and South West Africa

Locality *Coastal*	Years	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.	Yearly average
Lobito	1932–53	0·8	1·5	4·7	2·1	0·1	—	—	tr.	0·1	1·2	1·0	2·4	13·9
Mossamedes	1930–53	0·3	0·4	0·7	0·5	tr.	tr.	tr.	tr.	tr.	tr	0·1	0·1	2·1
Walvis Bay	1916–50	tr.	0·2	0·3	0·1	0·1	tr.	tr.	0·1	tr.	tr.	tr.	tr.	0·9
Inland														
Sâ da Bandeira 5,860 feet	1932–53	5·9	6·2	6·6	3·7	0·1	tr.	—	—	0·2	2·8	4·4	6·3	36·2
Ondonga, 3,593 feet	1902–50	4·3	4·8	3·7	1·4	0·1	—	tr.	tr.	0·1	0·5	1·8	3·6	20·3

* Rainfall figures for Gabela refer to the town on top of the escarpment, not to the forest on the face where the precipitation is higher.

Compiled from the Meteorological Office Tables of Temperature, Relative Humidity and Precipitation for the World, Pt. IV, 1958, with additional figures supplied by the Meteorological Office, Harrow, and by Mr. O. Kroel for Quimberima.

growth and bushes. Unfortunately, Heinrich (1958) has few records of breeding activity for the same species collected at Gabela ; such as there are conform with the general pattern of our collections, with young birds of *Spermophaga ruficapilla* collected at the end of July, and other species noted as having inactive gonads in August. On the other hand, he records breeding activity in several of the same species collected in similar forest further to the north at Canzele in March/April, most notably young birds then being found of *Dyaphorophyia concreta, Lanius mackinnoni* and *Camaroptera brevicaudata.*

Passerines of Grasslands, Reeds and Open Country (Table III)

In the east and centre the larks, chats, pipits and long-claws of the grasslands at Luacano, Lake Dilolo, Vouga and along the road mostly appear to be summer breeders. The exceptions were the Red-Capped Lark, *Calendrella cinerea,* of which juveniles were collected early in August, and *Saxicola torquata* which was nesting at Vouga. The Cisticolas, without exception, were in non-breeding dress or in moult to breeding dress, showing themselves summer breeders, as Lynes found. Nests and eggs of *Petrochelidon rufigula* were found on the 10th August in contrast to the record from the Belgian Congo of breeding in April, and a specimen of *Hirundo senegalensis* in moult also suggests dry season breeding. The most surprising records however concern the bishops, widows and waxbills, among which are many young birds and adults moulting into non-breeding dress indicating a breeding season continuing at least into June. The same species in the southern Congo and Northern Rhodesia are mostly recorded as summer breeders finishing in May at the latest.

It is difficult to account for the contrasts and the similarities shown by different families in comparison with what is found in their relatives in adjacent countries, for example why the cisticolas should be normal and the bishops abnormal. The grass burning must inevitably affect the grassland birds ; this had mostly been completed in the east but was being carried out in August in the central highlands. It may be significant that it is the seed-eaters which had apparently finished breeding before the fires while the insect-eaters bred after the fires.

In the western grasslands among the few specimens collected was a young *Mirafra africana* in September, as well as the young Francolin already referred to.

On Mt. Moco the waxbills and cisticolas living in the rank grass of the mountain gullies also had contrasting breeding seasons, the waxbills breeding in winter (a number of young birds being obtained in August) and the cisticolas in summer.

Passerines of the Western Thornbush, Thickets and Semi-desert, (Table IV)

The number of specimens collected in the thornbush and tangled thickets on top of the escarpment in the south-west and on the road north from Lobito was limited, but it is apparent that the breeding season is very varied among the different species. In addition to the numbers of young spur-fowl seen and collected, young of *Laniarius bicolor, Fringillaria tahapisi, Apalis flavida* and *Alseonax cinereus* were collected in August, but other species, even in the same families, gave evidence of being summer breeders.

The pattern in the semi-desert of the coastal plain is very different, with a high proportion of species in very fresh plumage or post-breeding moult. In arid country such as this the plumage fades and abrades very quickly so that when a specimen is found to have very fresh colours and unabraded feathers it cannot long have completed moult and the breeding season can therefore be assessed with greater assurance than with birds living in more sheltered conditions. These birds collected in September seem likely to have bred in June/July, and are in comparable plumage to those collected in the Kaokoveld in May. This three months' difference was unexpected, since the dry coastal belt of Angola seems a natural continuation of the Namib and Vornamib of South West Africa with no natural barriers between (the break made by the Cunene can hardly have significance). It is too long also to consider as a further logical step in the retardation of the breeding season from south to north as noted by Macdonald.

However, the explanation may possibly lie in the rainfall figures for 1957, which show that in March and April there were exceptionally heavy rains at Lobito, 11·6 inches and 7·4 inches against an average over twenty-two years of 4·7 inches and 2·1 inches for the same months. The figures at Benguela are not so high, 7·6 inches in March and 3·3 inches in April, but are still exceptional for that coast. It seems quite probable that there would be heavy casualities among nests, eggs and young birds under these conditions, and that second broods were therefore reared. Data on breeding seasons in other years on this coast is badly needed before the problem is really understood ; a little is provided by specimens in the British Museum collected by Ansorge in 1905 among which are some of *Erythropygia paena*, *Plocepasser mahali* and *Passer motitensis* in post-breeding moult at the end of July, suggesting an earlier breeding season in 1905 than in 1957.

NEW RECORDS FOR ANGOLA AND EXTENSIONS OF RANGES

Species not Hitherto recorded from Angola

Francolinus albogularis meinertzhageni Luacano.
Francolinus sephaena zambesiae Leba.
Mirafra passerina Cahinde.
Macronyx grimwoodi Luacano area, Vouga.

Extension of Ranges in Angola

Poicephalus meyeri matschei Luacano (western extension).
Caprimulgus natalensis mpasa Lake Dilolo (western ext.).
Andropadus virens zombensis Luau R., Luacano (western ext.).
Alseonax c. cinereus 40 m. S. of Mumbondo (southern ext.).
Cossypha h. heuglini Luacano (western ext.).
Erythropygia leucosticta reichenowi Chingoroi (southern ext.).
Eremomela icteropygialis polioxantha Vouga, and 100 m. West of Vila Luso (western ext.).
Prinia subflava ovampensis Quipungo, Leba (northern ext.).
Campephaga q. quiscalina Chingoroi, (southern ext.).

Prionops gabela 40 m. S. of Mumbondo (second known locality).
Chlorophoneus nigrifrons manningi Luau R., (western ext.).
Cinnyris s. superbus Chingoroi (southern ext.).
Cyanomitra verticalis bannermani Luacano (western ext.).
Euplectes orix subsp? Lake Dilolo (northern ext.).
Lagonosticta rubricata congica Luau R., (western ext.).
Estrilda astrilde niediecki Vouga (northern ext.).
Hypochaera nigerrima Chingoroi (southern ext.).

New Races

It was found necessary to describe three new races, mainly on specimens from this collection. These were published in short papers as follows :—

Prodotiscus insignis lathburyi Hall, Bull. B.O.C. 78, 1958, p. 152 : Mt. Moco.
Mirafra angolensis antonii Hall, loc. cit. p. 153 : 5 m. east of Luacano.
Parus afer benguelae Hall & Traylor, Bull. B.O.C. 79, 1959, p. 12 m. SE. of Benguela.

Sight Records

Among species of interest seen but not collected were the Palm-nut Vulture, *Gypohierax angolensis*, common along the road between Lobito, Novo Redondo and the foot of the escarpment at Gabela. Hartlaub's Duck, *Pteronetta hartlaubii*, a pair on the Luau River; the Bustard *Eupodotis senegalensis mackenziei*, at Vouga; the Rufous-Bellied Heron, *Erythrocnus rufiventer*, about twenty-five of which spent the day in high reeds near a river at Lake Dilolo, flighting down to the main lake half a mile away at sunset. A few were also seen on a small lagoon on the Humpata plateau near Jau.

The Giant Blue Turaco, *Corytheola cristata*, was seen on the Luau River and at Gabela, both localities representing the southernmost limits of its range as known at present, the Luau River being an extension of the range shown by Moreau (1958 : map 4, p. 72).

Three other species seen at the southern limits of their ranges are Monteiro's Twinspot, *Clytospiza monteira*, at Gabela, the Shining Blue Kingfisher, *Alcedo quadribachys*, on the Luau River, and Boehm's Spinetail, *Neafrapus bohmi*, 80 m. south of Luanda.

SYSTEMATIC AND FIELD NOTES ON SELECTED SPECIES

In working on the systematics and taxonomy of the Angola collection the standard works on the birds of the neighbouring countries have all been consulted, Chapin (1932–1954) for the Belgian Congo, Benson & White (1957) for Northern Rhodesia, Hoesch & Niethammer (1940) and Macdonald (1957) for South West Africa, Roberts (1940) for South Africa—as well as the manuscript of Mackworth-Praed & Grant's " Birds of the Southern Third of Africa."

It is inevitable that all these authors do not always agree on systematic questions, especially the vexed one of " lumping " in genera and species. I have followed no author consistently, using my own preference where there are differences. On the generic and specific levels I am conscious that I have not always been able to study the problems as deeply as is necessary to form a considered opinion ; I have perhaps been influenced by my mistrust of over-enthusiastic lumping, which I feel has sometimes been proposed to evade the necessity of making a decision. It is not, to me, necessarily sufficient reason for uniting two genera, that one species may show characters of both.

The subspecific status of all forms listed has been studied on the evidence of specimens in the British Museum, supplemented in many cases by information and loans from other Museums, most notably from Mr. M. A. Traylor and the Chicago Natural History Museum, where a large part of the Angola collection from the American Museum of Natural History is temporarily housed.

The Systematic Notes include any revisions that appear necessary of the accepted range of status of the various forms, and some notes on moults and plumage of the less well-known species.

Most of the field-notes on sunbirds were supplied by John Williams, and the majority on all other birds by Tony Archer and General Lathbury. Williams was also responsible for most of the detailed notes on food, derived from the contents of stomachs and crops ; but in the case of the turacos, some francolins, and *Xenocopsychus*, detailed analysis of the seeds and insects was made in the Botanical and Entomological Departments of the Museum.

Since the collection was made papers have been published on collections from Angola by Heinrich (1958), and Meise (1958). These contain field or systematic notes on many of the species we obtained and in selecting species in the following notes I have endeavoured to avoid duplicating information and to concentrate on those in which some contribution can be made to present knowledge of the bird in the hand or in the field. Data on all other specimens are, however, readily available in the British Museum should they be required.

With so many standard works now available on African birds it has not seemed necessary to provide other reference than the author's name and date to the forms discussed unless they have been recently described or the names newly brought into use. Type localities and measurements are included only when relevant to the discussion.

2. **Francolinus swierstrai** (Roberts), *Ann. Trans. Mus.* 13, p. 72, 1929 : Mombolo, Cuanza Sul. (syn. *Francolinus cruzi* Themido 1937 : Hanha, Benguela dist.).

Specimens

1 ♂, 1 imm. ♂. Mt. Moco 7,000 feet, 17–22nd Aug. Bill and legs orange red ; iris hazel. Wing ad. 184, imm. moult ; bill 32, 30 ; tail 103, 84 mm.

Field Notes

This rare francolin was found in or near pockets of forest on the upper slopes. One was found pecking about among fallen leaves in the undergrowth, the other was flushed from the bank of a stream covered in thick bracken. It uttered a shrill harsh cry, not unlike that of *Francolinus jacksoni* O-Grant, and perched in a low tree. The crops contained seeds of two species of Leguminosae, one of which was a *Dolichos* or *Neorautanenia*, the other unidentified.

Systematic Notes

One of these specimens is an adult male with a long spur ; it is in worn plumage with some fresh feathers coming in on the head. The second is not quite fully adult, having a short blunt spur and some rusty edges to the wing-coverts, as described by Roberts for the type, which was also a young male. The young bird is mostly in fresh plumage with the primaries in moult and some fresh feathers coming in on the head. The gonads of both specimens were slightly enlarged.

3. ***Francolinus sephaena zambesiae*** Praed 1920 : Mesanague, Zambesi, P.E.A.

Specimen

1 ♀ Leba, 2nd Sept.

Systematic Notes

A soil-stained specimen but matching well in markings with the type and others of this race, of which *F. s. thompsoni* (Roberts) is considered a synonym.

4. ***Francolinus finschi*** Bocage 1881 : Caconda, Huila dist.

Specimens

1 ♂ 1 ♀ Mt. Moco 7,000 feet, 18–21st Aug.

Field Notes

These birds were collected and others were seen, often in pairs, in the Brachystegia woodlands on the upper slopes of the mountain, and on the bare slopes above the tree line. The female was one of a pair pecking about in burnt grass and leaves. The male had been feeding on buprestid beetles, larvae and beans.

Systematic Notes

These specimens have been compared with a male and female from Brazzaville, lent by the Museum d'Histoire Naturelle, Paris, and with a male in the British Museum from the watershed of the rivers Cuanza and Luando. The three latter are very similar in general appearance and in the extent of rufous in the wings. The Moco birds in comparison have less rufous in the wings, with none on the outer web of the first four primaries, and the rufous on the inner web not reaching to within 20 mm. of the tip on the first five primaries. It is possible that these differences may represent geographical variation.

7. **Francolinus albogularis (?) meinertzhageni** White, *Bull. B.O.C.* 65, 1944 p. 7 : Kumanu Plain, west Balovale, N. Rhodesia.

Specimens

2 ♂ 3 ♀ Plains near Luacano, 31st July–1st Aug.

Field Notes

Three of these White-throated Francolins were shot out of a covey of seven on an open grassy plain with no vegetation over a foot high. The others were a pair on a similar plain ; the female did not run or fly after the male had been shot. They had been feeding variously on beetles, grass seeds, small fishes and a small frog.

Systematic Notes

All are in worn plumage and stained with burnt grass. Even allowing for this the males appear to be darker, less rufous and more patterned with grey than the type of *meinertzhageni*. They show, in fact, much the same characters that distinguish the Luacano race of *Mirafra angolensis, M. a. antonii*, and it is possible that when better series are available from Angola and Rhodesia the Luacano francolins may also be found to represent a new race.

21. **Tauraco corythaix schalowi** (Reichenow) 1891.

Specimens

2 ♀ Mt. Moco 7,000 feet, 16th Aug.: 1 ♀ Leba, 2nd Sept.: 1 ♂ Chingoroi, 9th Sept.

Field Notes

It seems worth recording that at Chingoroi, where both *T. c. schalowi* and the Red-crested Turaco, *T. erythrolophus*, were found together, the crop of each was found to contain quite different types of seeds, that of *T. c. schalowi* being full of small black seeds, probably Molvaceae and possibly a species of *Sida*, and some unidentified flattened seeds ; that of *T. erythrolophus* seeds, possibly of the family Rubiaceae.

22. **Tauraco erythrolophus** (Vieillot) 1819.

Specimen

1 Chingoroi, 8th Sept.

Field Notes

This specimen was collected in not very thick forest bordering the stream. Others were seen later in the escarpment forest at Gabela. See under *T. c. schalowi* for crop contents.

Systematic Notes

Moreau (1958 : 104) includes Huila in the range of *T. erythrolophus* : he has asked me to make a correction to this since the specimen in the collection at Pittsburgh on which this was based is actually labelled " dist. Huila " and was collected the same day as another labelled " Chingoroi." Chingoroi lies just within the boundary of the Huila district : the Turaco has not otherwise been recorded further south than Chingoroi, nor does there seem suitable habitat for it, and that specimen must therefore be presumed to have come from Chingoroi.

33. **Otus scops senegalensis** (Swainson) 1837 : Gambia.

Specimen

1 ♂ 20 m. NE. of Novo Redondo, 14th Sept. Wing 125 mm.

Systematic Notes

This is a very small Scops Owl, very sandy in tone with fine vermiculations. In the British Museum it can be matched for colour with a specimen from Cape Town and several from West Africa. It seems very doubtful therefore if there are grounds for recognizing races on colour in a species with so much individual variation and I follow Mackworth-Praed and Grant (1952 : 650) in considering the majority of African Scops Owls as *O. s. senegalensis*. This sandy specimen refutes the suggestion that birds of western Angola can be recognized as a distinct grey race, *O. s. hendersoni* (Cassin), the type of which was obtained at sea off Novo Redondo.

36. **Ciccaba woodfordii bohndorffi** (Sharpe) 1884 : Semmio, Niam-Niam country, Belgian Congo.

Specimen

1 ♂ Luau R. 29th July.

Systematic Notes

Mackworth-Praed & Grant (1958 : 333) have already noted that, on the British Museum series of African Woodowls, there are ample grounds for recognizing *C. w. bohndorffi* as distinct from the darker *C. w. nuchalis* (Sharpe) of West Africa. This specimen fits well with the series of *bohndorffi* being a bright rufous, lighter on the mantle than any West African bird examined.

37. **Semeiophorus vexillarius** (Gould) 1838.

Specimen

1 ♂ Vouga, 11th Aug.

Systematic Notes

An unusually early record for a Pennant-winged Nightjar in the southern part of the continent. The pennants are still in sheath but nearly full grown (638 mm.).

38. ***Caprimulgus natalensis (?)mpasa*** Smithers, *Bull. B.O.C.* 74, p. 84, 1954 : Mpasa, Luwingu dist. N. Rhodesia.

Specimen

1 ♂ Lake Dilolo, 4th Aug.

Systematic Notes

On the upper parts this White-tailed Nightjar is a very close match with one from Balovale and slightly less grey than others from north-eastern N. Rhodesia. Below it has only traces of barring on the sides of the chest, unlike the heavily barred Rhodesian birds, and nearer in this character to the type of *C. n. fulviventris* Hartlaub, from Bembe, which differs otherwise in being rufous with light markings above.

39. ***Caprimulgus fossii*** Hartlaub 1857 : Gaboon.

Specimens

2 ♂ 2 ♀ Lake Dilolo, 5th Aug.

Systematic Notes

I follow Mackworth-Praed and Grant (1952 : 677) in not recognizing any races of the Gaboon Nightjar though I am not wholly convinced that a detailed study of a considerable series will support this view. From the available series it would appear that the population of Gaboon is consistently small with wings under 150 mm. and that all birds from the western parts of Africa tend to be greyer and less heavily marked than those from the east. At the same time individuals are found in South Africa as small as those of Gaboon and matching them in colour. If it is found necessary to recognize races our birds would probably be *C. f. welwitschii* Bocage.

41. ***Caprimulgus poliocephalus koesteri*** Neumann 1931 : Sandula, S. of Cassongue, Cuanza Sul/Huambo border.

Specimen

1 ♂ Mt. Moco 7,000 feet, 20th Aug. Wing 151, bill 19, tail 113 mm.

Field Notes

"Hawking from a dead branch over thick grass, bush and bracken bordering a small stream in the late evening." The stomach contained three beetles.

Although the single specimen was actually collected outside the forest patches it has been included among forest birds in the Tables since, from the known habits of other races, it seems likely to be associated with the forest.

Systematic Notes

I believe this to be only the second known specimen of *koesteri* and the first known male. Mr. J. C. Greenway kindly compared it with the type in the Museum of Comparative Zoology, Cambridge, Mass. and found that it differed only in having the outer webs of the first and second primaries more profusely spotted with pale brown, in having the seven pale brown bars on the inner webs of the outermost tail feathers more distinct, and in having the white tip of the outer tail feather larger, 53 mm. against 30 mm. All these differences are consistent with sexual variation and he confirms my view that the type of *C. koesteri*, which was unsexed but presumed to be a male, is probably a female.

Chapin (1939 : 413) was the first to suggest that *koesteri* might be conspecific with the Abyssinian Nightjar, *C. poliocephalus* Rüppell, and the forms *ruwenzorii* O-Grant, and *guttifer* Grote, of south-west Tanganyika and Nyasaland, all of them being exclusively mountain birds associated with montane forest. The Moco bird is, in fact, a very close match with the type of *ruwenzorii* which differs only in having rather more white on the throat and tail.

The type locality of *koesteri* has been given variously as " Chipepe, Bailundu," " Lebule, near Luimbale," and as " Luimbale." Mr. Greenway wrote me that Koester in a letter to Dr. Chapin in 1947 stated that the correct type locality is Sandula, south of Cassongue (about lat. 12° 15′ S.; long. 15° E.), at about 1,800 m.

43. ***Heterotrogon vittatus camerunensis*** Reichenow 1902 : Cameroons.

Specimens

1 ♂ 1 ♀ Mt. Moco 7,000 feet 18–21st Aug. Wing ♂ 123, ♀ 124 ; tail ♂ 150, ♀ 145 mm.

Systematic Notes

The two races of Bar-tailed Trogon generally recognized are distinguished on size. These two birds, and one quoted by Chapin (1939 : 486) from Moco with a wing of 122 mm. are rather larger than typical *camerunensis*, but best placed with it.

44. ***Apaloderma narina*** subsp. (?).

Specimen

1 ♀ 12 m. S. of Gabela, 18th Sept. Wing 133 ; tail, second innermost rectrices 143, central pair in moult.

Systematic Notes

Other trogons collected at Quela, Gabela and Huila have been referred to *A. n. brachyurum* Chapin, by Heinrich (1958 : 335) but one from " Amboim " (i.e. Gabela) discussed by Sick (1934 : 168) is possibly intermediate between *A. n. brachyurum* and *A. n. narina*. Our Gabela female is short-tailed, as *brachyurum*, but closest to *narina* in the colour of the breast and chin, which are a clear light brown with rufous tinges, but it differs from most specimens of *narina* in having only a faint suggestion of the greyish band that usually separates the pink of the abdomen from the breast.

45. ***Colius striatus congicus*** Reichenow 1923 : Lupungum, in Lomamu dist. Belgian Congo.

Specimen

1 ♂ Luau R., 30th July.

Systematic Notes

This Speckled Mousebird agrees in all repects with *C. s. congicus*, and the colour of the iris was noted as being apple green.

47. ***Colius castanotus*** Verreaux 1855.

Specimens

2 ♂ 2 ♀ 1 juv. ♂ Mt. Moco 6,000–6,500 feet : 1 ♂ Chingoroi 8th Sept. 1 ♂ 20 m. NE. of Novo Redondo, 14th Sept.

Field Notes

The Red-backed Mousebird was fairly common on Mt. Moco in the forests and woodlands, it was also common where the Novo Redondo-Gabela road ran through hilly country with a covering of *Euphorbia* and thorn trees.

Systematic Notes

The young bird differs from the adults in having light red-brown edges to the wing-coverts and a dark brown, instead of a yellow-green, eye.

48. ***Lybius torquatus bocagei*** (Sousa), *Jorn. Ac. Real. Sci. Lisboa*, 11, p. 958, 1886 : Caconda, Huila dist.

Specimens

1 ♂ 1 ♀ Luau R., 28–30th July : 3 ♂ Mt. Moco 6,000 feet, 21st Aug. Wings 4 ♂ 89–94, ♀ 88.

Field Notes

One male collected on Mt. Moco was found, when collected, to have its tail bent sideways, presumably from incubating in a confined space since it is in post-breeding moult. The other two Moco birds are in worn plumage.

Systematic Notes

Clancey (1956 and 1958) has reviewed the races of the Black-collared Barbet in southern Africa. I cannot agree with him that variation over this area is great enough to warrant the recognition of five races. Treating the species on broader lines I would recognize (1) *L. t. torquatus* (Dumont) from South Africa, distinguished by the yellow of the underparts being mixed with darker markings and vermiculations. (2) *L. t. bocagei*, synonym *L. t. congicus* (Reichenow), of Angola east to Luau R., with underparts less heavily marked than *torquatus*. (3) *L. t. zombae* Shelley, synonyms *L. t. lucidiventris* Clancey, and *L. t. pumilio* Grote, from Nyasaland, southern Congo, the Rhodesias, N. Bechuanaland, Portuguese East Africa and parts of Tanganyika, with clear yellow underparts.

The five specimens obtained have all some dark vermiculations below and match well with a Caconda specimen in this respect. Above they show considerable individual variation particularly between the male and female from Luau R. the male being greyish on the mantle and coarsely vermiculated, the female brownish and finely vermiculated ; this variation does not seem to be sexual.

49. (a) ***Buccanodon anchietae anchietae*** Bocage 1869 : Caconda, Huila dist.
    (b) ***Buccanodon anchietae rex*** Neumann 1908 : Duque de Bragança, Malanje dist.
    (c) ***Buccanodon anchietae katangae*** Vincent 1934 : Kaluli R. Katanga.

Specimens

(*a*) 1 Caconda, 27th Aug.: (*b*) 1 ♂ Mt. Moco 6,000 feet, 18th Aug.: (*c*) 1 ♂ 20 m. N. of Lake Dilolo, 3rd Aug.: 1 ♂ 1 ♀ 28 m. N. of Vila Luso, 8th Aug. Wings (*a*) 95. (*b*) 1 ♂ 94. (*c*) 2 ♂ 87–88, 1 ♀ 88 mm.

Systematic Notes

On these specimens the three races of Anchietas Barbet are recognizable on the colour and pattern of the yellow on the crown. In *anchietae* and *rex* the yellow is purer, less greenish than in *katangae*, and in *rex* it does not extend to the hind crown which is solid black. There are no topotypical specimens of *rex* in the British Museum and this is the first to answer to the description. Chapin gives the Bailundu district within the range of *rex* and it is probable that Moco is on the southern limit since another specimen from there in the Museum has not got the characters so well defined. The extent of yellow on the breast is slightly greater in *katangae* than in the other specimens.

50. ***Gymnobucco calvus vernayi*** Boulton 1931 : Mombolo, Cuanza Sul.

Specimens

2 ♀ Mt. Moco 7,500 feet, 20th Aug.

Field Notes

One of these Naked-faced Barbets was collected from a party of three in a forested valley. It had been eating crickets and beetles but no fruit.

53. ***Viridibucco coryphaea angolensis*** Boulton 1931 : Mombolo, Cuanza Sul.

Specimens

1 ♂ 1 ♀ Mt. Moco 7,000 feet, 17th Aug.

Field Notes

Although this Tinker-bird is normally associated with mountain forest one bird was found away from the forest patches in some small isolated trees in open rocky country. It drew attention to itself with a soft piping call. It had been feeding on *Loranthus* fruits.

Systematic Notes

The female was preserved in salt : in comparison with the male it is greyer below lacking the yellow green wash, and above the yellow on the mantle and nape is paler appearing rather bleached. In my opinion these differences may be due to the action of the salt, since no sexual differences have been recorded in this species and none are apparent in a series of the nominate race.

55. (a) ***Indicator minor minor ≷ conirostris***
(b) ***Indicator minor damarensis*** (Roberts) 1928.

Specimens

(*a*) 1 ♂ Luacano, 3rd Aug.: (*b*) 1 ♀ Leba, 31st Aug.

Systematic Notes

The specimen from Luacano is interesting since it shows some approach to the darker more heavily streaked form *conirostris*, that was long considered a distinct species, and I have been fortunate in being able to discuss with Dr. H. Friedmann some of the problems of relationship between the two forms and to examine with him the series in the British Museum. Specimens have also been borrowed from Tervuren and Chicago. *I. m. conirostris* (Cassin), is a bird of the tropical forests of West Africa and the Congo and is found also in isolated pockets on Ruwenzori and Mt. Elgon within the range of other forms. Surrounding the range of *conirostris* are more lightly streaked forms living in savannah woodlands, *I. m. riggenbachi* Zedlitz, of West Africa to the Sudan, *I. m. minor* Stephens, of East and South Africa, and *I. m. damarensis* of South West Africa, the palest form. Between the two groups from localities encircling the range of *conirostris*, individuals have been taken which show some intermediate characters. Some of these from the base of Ruwenzori have been recorded by Chapin (1939 : 543), others from Owerri in southern Nigeria were described as *I. conirostris pallidus* Marchant. Other specimens showing intermediate characters in some degree have been examined from Tibati, N. Cameroons ; Ibembo, Lower Uelle ; Tembura, Bahr-el-Ghazal district, Sudan ; Kabalo, Tanganyika district, eastern Belgian Congo ; Kasaji, south-western Belgian Congo ; Luacano ; Mt. Soque, near Luimbale, central Angola. The Luacano bird was collected on the edge of the riverine forest ; birds in the type series of *pallidus* were recorded as confined to high forest or broken forest ; the bird from Mt. Soque was collected in montane forest (Heinrich 1958 : 336) ; it therefore seems possible that all the intermediates are associated with some type of forest, or remnant of forest, rather than with woodland. This would perhaps account for the presence at Tibati of two apparently different forms, the intermediate specimen already referred to, and the type of *riggenbachi*. This type has not been examined since it was matched by Chapin (loc. cit.) with a specimen in the British Museum from the Shari River.

There seems little to be gained by attempting to give subspecific status to the isolated intermediate specimens. The name *I. m. pallidus* could perhaps be used to cover all the intergrades but the Nigerian birds are closer to *conirostris* than most of the others. I prefer to leave the rest under intermediate designations according to their proximity, both in appearance and locality, to other races

Other specimens examined from Angola are from Catumbela and Malanje, both of which are readily identified as *I. m. minor*. The one obtained at Leba in mixed scrub by the stream is, however, slightly paler and seems to match best with *I. m. damarensis* of South West Africa. It seems possible that *damarensis* is therefore associated exclusively with thorn country.

59. *Campethera cailliautii fulleborni* ≷ *permista*

Specimens

1 ♂ Luau R. 31st July. 1 ♀ near Vila Luso, 7th Aug.

Systematic Notes

Chapin (Ibis 1952 : 535) discusses intermediates between the barred Green-backed Woodpecker, *Campethera permista* (Reichenow), and the Little Spotted Woodpecker, *Campethera cailliautii* (Malherbe), found at Baraka on Lake Tanganyika, also at a locality 340 miles west of Baraka, and at Katombe (6° 29′ S.: 23° 58′ E.). The Angola specimens are yet other intermediates though closer to the Little Spotted Woodpecker, represented in north-western Rhodesia by the race *C. c. fulleborni* (Neumann). On the mantle the round spots of typical *fulleborni* are replaced by small elongated spots : on the underparts the round black spots of the breast are replaced by kidney-shaped spots almost stretching to each edge of the feather, each one being twice as broad as it is deep. The kidney-shaped spots are more elongated in the male than the female. The general effect is of a bird more heavily marked below and more lightly marked above than *fulleborni* ; less heavily marked below and more heavily marked above than *permista*. The occurrence in eastern

Angola of intergrades and ones closer to *C. c. fulleborni* seems logical since *C. p. permista* is found in northern Angola at Vila Salazar and *C. c. fulleborni* rather nearer, in the Balovale area of northern Rhodesia.

60. ***Campethera nivosa herberti*** (Alexander) 1908 : Bwande, Ubangi R. Belgian Congo.

Specimen

1 ♂ 12 m. S. of Gabela, 18th Sept.

Systematic Notes

Meise (1958 : 70) has described a new race of the Buff-spotted Woodpecker, *C. n. canzelae,* from Canzele, about 200 miles north of Gabela. This male from Gabela is a very close match with the type of *C. n. herberti* ; it is the only Angola specimen of the species in the British Museum, but Mr. Traylor (in litt.) tells me that he, on specimens in Chicago, considers more northern birds to be *herberti* also, and that *canzelae* therefore should be regarded as a synonym of *herberti.*

61. (a) ***Dendropicos fuscescens hartlaubii*** Malherbe 1849 : Zanzibar.

(b) ***Dendropicos fuscescens hartlaubii ≷ stresemanni*** Grote 1922 : Okaukweyo, SW. Africa.

Specimens

(*a*) 1 ♂ Luau R., 30th July : 1 ♀ 20 m. SE. of Luacano, 6th Aug. : 1 ♀ 15 m. N. of Vila Flor, 25th Aug.: 1 ♂ 5 m. S. of Caconda, 28th Aug. (*b*) 1 ♂ 1 ♀ Quipungo, 28–29th Aug.

Field Notes

All the specimens of (*a*) were collected in Brachystegia and the pair of (*b*) in thorn country.

Systematic Notes

The use of the name *hartlaubii* for widespread populations of the Cardinal Woodpecker was discussed (Hall, 1956 : 101) ; these specimens together with others in the British Museum help to complete the picture in Angola. They show that birds from the Vila Salazar area in the north of Angola are consistently washed with yellow on the mantle, matching a series from Tanganyika ; those from the centre of the country are variable, the Luau R. male and a Caconda male of an older collection being washed with yellow although ours from Caconda is not ; those from the thorn country in the south show a very marked approach to the lightly streaked *stresemanni* of South West Africa this being particularly true of the Quipungo male although the female is more heavily streaked.

62. ***Mesopicos griseocephalus persimilis*** Neumann 1933 : Chipepe, Cuanza Sul.

Specimens

1 ♂, 2 imm. Mt. Moco 7,000 feet, 20–21st Aug.: 1 imm. Leba, 3rd Sept. Wings 101–106.

Field Notes

The Olive Woodpeckers on Moco were shot in or near the forest, one of the young being in a party of three. The Leba bird was one of a party of four associated with a mixed bird party of greenbuls and *Lanioturdus torquatus*, moving among the stunted woodland on the hillside above the gorge of the river.

Systematic Notes

These are the first Angola specimens in the British Museum, and on them the race *persimilis* has been accepted tentatively as distinct from *ruwenzori* Sharpe, since they are all short winged in comparison with *ruwenzori*. There are no colour differences apparent between the single adult *persimilis* and eastern birds but it is a specimen which was preserved temporarily in salt and therefore not very satisfactory for comparison.

64. (a) ***Mirafra africana kabalii* White,** *Bull. B.O.C.* 64, p. 20, 1943 : Minyanya Plain, Balovale.
(b) ***Mirafra africana occidentalis*** (Hartlaub) 1857 : Gaboon.
(c) ***Mirafra africana occidentalis* ≷ *pallida*** Sharpe.

Specimens

(*a*) 2 ♂ 2 ♀ Luacano area, 31st July–1st Aug.: (*b*) 1 ♂ 1 ♀ Quipungo, 29th Aug.: 1 ♂ 1 imm. ♂, 60–80 m. N. of Lobito, 14th Sept.: (*c*) 1 ♂ Leba, 4th Sept.

Field Notes

The late Captain Grant always expressed some doubts as to whether the form *kabalii* was really a race of the Rufous-naped Lark and it was hoped to obtain some field evidence on this point for him. Unfortunately, at Luacano these larks were apparently rare and were not observed long enough for conclusions to be reached ; they were not heard calling. In the areas of western Angola where specimens of the western race were collected they were common and prominent, sitting on convenient perches, sometimes uttering typical "*africana*" whistles, and going to ground and running when disturbed. The apparent difference in behaviour between the two races might be partly attributable to different breeding seasons, some western birds being in worn plumage with enlarged gonads, but must also be partly due to the absence of suitable perches on the Luacano plains. It seems likely that *kabalii* must have adapted itself to a more terrestrial mode of life than other forms and it would be interesting to observe its behaviour in the breeding season and see how it is modified to the rather different conditions.

Systematic Notes

The contrast in appearance between the specimens of the west and east of Angola is certainly striking. Those of the west have the long bill, rufous nape patch and typical lark mantle and head. The bills of the eastern birds are variable, but mostly short, they are almost blue-grey on the mantle with the dark centres to the feathers wider, to give a more scalloped effect : the rufous nape patch for the same reason is inconspicuous in three out of the four.

Western birds from north of Lobito south into South West Africa show a cline from greyer birds in the north (*occidentalis*) to paler and more rufous birds in the south (*pallida*) ; the Leba specimen is intermediate, as one from the Kaokoveld was also found to be by Macdonald and Hall (1957 : 18) ; it seems that both represent steps in the cline.

The eastern birds from Luacano match well with a topotype of *kabalii*. White (1956 : 122) refers to *kabalii* two specimens collected by Lynes from Missao de Luz (140 m. west of Luacano) and from about 190 m. further north in the Lunda district. They are both redder than typical *kabalii* and seem to me to be intermediate between this race and *malbranti* Chapin, of the French Congo, as represented by another Lynes' bird from Petianga, Kasai district ; *malbranti* in turn has close affinities with *stresemanni* Bannerman, of the Cameroon highlands and *kurrae* Lynes, of Darfur. These links between *kabalii* and northern races of *M. africana* seem to provide convincing evidence that it should be considered conspecific with them, all forming a rather distinctive group in pattern and size within the species as a whole.

65. (a) ***Mirafra angolensis angolensis*** Bocage 1880 : Caconda, Huila dist.
(b) ***Mirafra angolensis antonii*** Hall 1958 : 5 m. east of Luacano, Moxico.

Specimens

(*a*) 3 ♂ 1 ♀ Vouga, 11th Aug.: 1 ♀ 50 m. E. of Vila General Machado, 9th Aug.: 1 ♂ Mt. Moco 6,000 feet 16th Aug.: (*b*) 6 ♂ 3 ♀ Luacano area, 1–3rd Aug.

Field Notes

All were collected on open plains, usually near the wetter valleys or ditches rather than on the dry open spaces (see p. 394). They were in pairs or single. The flight was noted as being low and straight and birds put up flew some distance before settling again. One was seen to plane down from a height and perch on an anthill.

Systematic Notes

The systematics of the Angola lark were discussed when *M. a. antonii* was described.

74. **Anthus vaalensis neumanni** Meinertzhagen 1920: Ambaca, Cuanza Norte.

Specimens

1 ♀ Lake Dilolo, 6th Aug.: 1 ♀ 43 m. W. of Texeira de Sousa, 31st July: 1 ♀ 14 m. W. of Munhango, 9th Aug.: 2 ♂ 1 ♀ Vouga, 10–11th Aug.: 1 ♀ Nova Lisboa, 13th Aug.: 1 ♂ Leba, 2nd Sept.: 2 ♀ Humpata-Jau road, 4th Sept. Wing 3 ♂ 92–100, 7 ♀ 92–102: hind claw ♂♀ 9–12 mm. Bill colour, dark brown or blackish above, pale below with yellow gape.

Field Notes

All these pipits were found in fairly open ground, often in the vicinity of water or marsh. On the Vouga plains they were alongside *Mirafra angolensis* on the slopes above the marshy valleys, rather than with the Longclaws in the bottom of the valleys.

Systematic Notes

The identification of the Plain-backed Pipits of Angola was discussed in a recent paper (Hall, 1959) in which it was shown that it is not practical to recognize more than one race of *A. vaalensis* in Angola, although there is some geographical variation. Of these specimens all from Vouga and further east are rather greyer than those from the west, the differences not entirely due to the fact that the eastern birds are slightly stained from burnt ground.

75. **Anthus leucophyrs bohndorffi** Neumann 1906: Kassongo, Belgian Congo.

Specimen

1 ♂ Mt. Moco 6,500 feet, 18th Aug. Wing 1 ♂ 102: hind claw 12·5 mm. Bill colour, blackish above, bright yellow below with darker tip.

Field Notes

It is not possible on this single specimen to form any opinion on the ecological relationship between the two Plain-backed Pipits in Angola. This bird was collected in a grassy patch by a stream at the base of the mountain.

Systematic Notes

This is one of the three rather long-winged and short-clawed representatives of *A. l. bohndorffi* found in the mountains, which were discussed in the paper on identification. (Hall, 1959). The bright yellow of the bill was very noticeable in the fresh skin and may possibly be a character of breeding dress.

76. **Anthus similis schoutedeni** Chapin 1937: Kwamouth, Belgian Congo.

Specimens

1 Mt. Moco 6,000 feet, 18th Aug.: 1 near Vila Flor, 25th Aug.: 1 ♂ Caconda, 28th Aug.

Field Notes

All were collected in Brachystegia woodland between 5,000 feet and 6,000 feet. It seems that in central Africa *Anthus similis* is more a bird of the woods than of the rocks, and both the common names applied to the species—Long-billed Pipit in Africa or Rock Pipit in Asia—are equally unsuited to this race, *schoutedeni* being comparatively short-billed (15–17 mm.).

77. ***Anthus lineiventris*** Sundevall 1850.

Specimen

1 ♂ Mt. Moco 7,000 feet, 21st Aug.

Field Notes

This bird was shot in a low tree on the edge of light woodland and the open rocky slopes. Chapin (1953 : 80) gives 5,000 feet as the altitudinal limit for the Striped Pipit.

78. ***Macronyx ameliae*** De Tarragon 1845.

Specimens

1 ♂ 2 ♀ 1 imm. ♀ Luacano area, 31st July–3rd Aug.: 1 ♂ Lake Dilolo, 4th Aug.: 2 ♂ Vouga, 10–11 Aug.

Notes on Moults

In the British Museum there are a number of specimens of Amelia's Longclaw collected by Lynes, Vincent and Benson which have good data on the condition of the gonads. From these, and from our birds, it is evident that in *M. ameliae* (and in *M. grimwoodi* as well) there is an irregular and incomplete moult before the breeding season. This moult, as with many pipits, may be of body plumage only or include some secondaries and/or the central rectrices. In the males new bright red feathers come in on the throat, replacing orange or buff feathers. From the one specimen examined in full post-breeding moult (Dedza, Nyasaland, 21st April) I am of the opinion that the bright red throat feathers are then replaced by orange-pink feathers, and that therefore some of the differences in the colour of the throat and abdomen are due to distinctive breeding and non-breeding plumages as well as to wear and individual variation, and differences in immature and adult plumages as discussed by White (1946 : 79).

79. ***Macronyx grimwoodi*** Benson 1955 : Chitunta Plain, Mwinilunga, N. Rhodesia.

Specimens

1 ♂ 36 m. W. of Texeira de Sousa, 31st July ; 3 ♂ 1 ♀ Vouga 10–11th Aug.

Field Notes

The first specimen was found on an open dambo near a river, and at Vouga others were found in the same marshy valleys as *M. amelia* and *M. fulleborni* Reichenow. The flight was noted as being slow with the white wing-patch conspicuous.

The discovery of Grimwood's Longclaw as far west as Vouga is a notable extension to its known range.

Systematic Notes

The colour of the throat in all specimens is richer than in one of the original type series which was described as " very pale." In all the Vouga birds new feathers are coming in on the throat and, in the two specimens in which this moult is most fully advanced, the general colour is rich salmon. These specimens also have a distinct pink flush on the abdomen and shoulders ; one is in body moult (see notes on moults of *M. amelia*).

From one of the Vouga birds specimens of feather lice were obtained which were identified by Dr. T. Clay as of the genus *Ricinus*.

84. ***Malacocincla fulvescens dilutior*** White, *Bull. B.O.C.* 73, p. 96, 1953 : Ndala Tando, Cuanza Sul.

Specimens

3 ♂ 12 m. S. of Gabela, 17–19th Sept. Wing 71–73.

Systematic Notes

When *dilutior* was described it was compared only with the nominate race. In appearance it seems closer to *ugandae* (van Someren), but has the throat paler, with distinct streaks and the chest bright buff rather than grey buff. It is also smaller, the wings of six males being 71–76 against 76–80 mm. for seven males of *ugandae*. The Gabela specimens are smaller than those from Vila Salazar (74–76).

89. ***Chlorocincla f. falkensteini*** (Reichenow) 1874.

Specimens

1 ♂ Chingoroi, 9th Sept. 1 ♀ 1 imm. ♀ 12 m. S. of Gabela, 17th Sept.

Systematic Notes

The young bird was identified as immature by the skull not being fully ossified, by having soft edges to the gape which was yellow, and by having a light brown, not " crimson " or " deep brick red " iris, but the plumage is similar to the adults. The stomach contained large berries which were possibly coffee.

93. **Phyllastrephus fulviventris** Cabanis 1876.

Specimens

1 ♂ 1 ♀ 1 Chingoroi, 8–10th Sept.: 1 ♂ 1 ♀ Gabela, 18–19th Sept.

Field Notes

Very little is yet known of this greenbul. These specimens were collected or netted in forest. One was in a party of three seen hopping about in the leaves and low undergrowth. Two were found to have been eating insects ; this seems to be the usual diet of *Phyllastrephus*, as noted by Chapin for the species *P. fischeri* (Reichenow), *P. xavieri* (Oustalet), *P. icterinus* (Bonaparte), *P. albigularis* (Junge) and *P. flavostriatus* (Sharpe).

96. **Alseonax c. cinereus** (Cassin) 1857.

Specimen

1 imm. ♀ 40 m. S. of Mumbondo, 20th Sept. Wing 69 mm.

Systematic Notes

This young flycatcher still has some juvenile plumage on the head and wing-coverts but gives the appearance of being fully grown. By its colour as well as by its small size it can confidently be referred to this race and not to the larger and paler *A. c. cinereolus* (Finsch & Hartlaub), which occurs in southern Angola.

105. **Hyliota australis ? slatini** Sassi 1914 : Beni, eastern Belgian Congo.

Specimens

1 ♂ 5 m. W. of Munhango, 9th Aug.: 2 ♂ 1 ♀ 28 m. W. of Vila Luso, 8th Aug.

Systematic Notes

White (1957 : 35) discusses variation in this flycatcher, with particular reference to the amount of white in the tail. There is very little available material of any races and the tail pattern of the male is the chief character on which races have been separated. From material in the British Museum, and information given to me by Miss Patterson on the birds in Bulawayo it seems that *H. a. australis* Shelley, with some white on both the inner and outer webs of the outer rectrices, is confined to Southern Rhodesia : *H. a. inornata* Vincent, from Portuguese East Africa and southern Nyasaland, is probably separable on having rather more white on the inner webs : birds from Northern Rhodesia are variable, often lacking any white, and the population there is apparently intermediate between *australis* and the wholly black-tailed *slatini* of the eastern Belgian Congo. Males from the southern Belgian Congo and the series from eastern Angola also are wholly black-tailed. The Amani race *usambara* Sclater, has a little white on the outer web but is chiefly distinguished by the richer colouring of the throat and breast.

Two eastern Congo birds were borrowed from Tervuren to compare with the Angola series. They were found to have rather a more purplish sheen on the upper parts, the Angola birds being a very sooty black, and to be more washed with orange on the breast. These differences could well be due to wear, the Angola series being in worn plumage and stained with burnt grass ; all are therefore referred for the present to *slatini*.

108. ***Batis pririt*** (Vieillot) 1818 : Lower Orange River.

Specimens

1 ♂ 18 m. W. of Cahinde, 5th Sept.: 1 ♂ 2 ♀ 12–30 m. SE. of Benguela, 11–12th Sept.

Systematic Notes

Pririt Flycatchers from Angola average smaller than those from the rest of the range ; but in the absence of any other distinguishing characters the difference does not seem great enough to warrant them being separated as a new race.

Comparative Wing Measurements

Angola	8♂	53–55	8♀	52–55
Damaraland	5♂	55–60	7♀	54–59
Namaqualand	8♂	57–59	5♀	56–57
Cape Prov.	3♂	56–58	3♀	56–57
Bechuanaland	6♂	55–58	8♀	54–58
O.F.S.	—	—	1♀	55

109. ***Batis m. margaritae*** Boulton 1934 : Mt. Moco, Benguela.

Specimens

2 ♂ 1 ♀ Mt. Moco 7,000–7,500 feet, 17–21st Aug.

Systematic Notes

Some doubt has been expressed as to whether *B. kathleenae* White, of Mwinilunga, is distinguishable from *margaritae*. Comparison of these Moco birds with *kathleenae* show that they differ in both sexes in being darker, more blue-grey on the back, and the blue-black of the eye-stripe and ear-coverts continues on to the hind neck to form an almost complete V. In addition the female *kathleenae* has the chestnut wing-coverts less rich and has a white line from the lores to the eye which is absent in the female *margaritae*.

In a genus such as *Batis* where the colour and pattern of the female is the most striking difference between species, I am not convinced that two forms such as *margaritae* and *kathleenae* with almost wholly black-and-white females should be united, as has been done, with *Batis capensis* (Linnaeus), in which the female has chestnut underparts and a browner grey back than the male. I prefer to consider *B. margaritae*, *B. capensis* and *B. diops* of Ruwenzori as forming a superspecies.

112. ***Dyaphorophyia concreta ansorgei*** Hartert 1905. Cabeça de Ladroes, Benguela.

Specimens

3 ♂ 3 ♀ 1 juv. ♂ Chingoroi, 8–11th Sept.: 1 ♂ 1 ♀ 12 m. S. of Gabela, 12th Sept.: (1 ♀ in spirit).

Field Notes

The Yellow-bellied Wattle-eye was most commonly netted in thick undergrowth of the forests. On one occasion two pairs and a party of three were seen within fifty yards, on another occasion one was seen with a party of *Chlorocichla flaviventris*. Several calls were noted, a sweet whistle " pih, pih, puh, puh, puh, puhh," preceded by a call not unlike an alarmed Yellow-vented Bulbul ; also a whistle " phee, phee, pheeat." The wings make a loud snap in flight.

Systematic Notes

The Chingoroi series are nearly topotypical : in view of the rapidity with which the colours fade it seems advisable to give a detailed description of the plumages of both sexes and the young bird. All the adults are finishing moult and show that both sexes have olive green backs when fresh, which wear to grey, with no metallic wash except on the tail. Below the males are a brilliant orange-yellow, the females very slightly paler on the abdomen with a rich chestnut throat and chest. The young male is mostly out of the nestling plumage which was described by Meise (1958 : 76). It is rather paler olive green on the back than the adults, has a pale yellow abdomen and a faint wash of orange on the chest and throat ; the wing-coverts and secondaries are tipped with buff ; the tail is grey with only a faint metallic tinge. The iris of the adults was noted as being dark brown with a silver thread round the pupil ; this thread was lacking in the young bird which had a greyish brown iris.

Meise (loc. cit.) has described a new race from Canzele in which females are greyer than in *ansorgei*. The Gabela specimens show no approach to this.

114. ***Tchitrea viridis plumbeiceps*** (Reichenow) 1898 : Malanje.

Specimens

1 ♂ 1 ♀ Vouga, 12th Aug.: 1 ♂ 1 ♀ Mt. Moco 7,000 feet, 20–21st Aug.

Field Notes

The pair at Vouga were among the few birds seen in Eucalyptus plantations along the railway. The pair from Mt. Moco were netted in thick montane forest but others were common in the Brachystegia of the foothills, and on one occasion were seen mobbing a Yellow-throated Sparrow.

Systematic Notes

See following species.

115. ***Tchitrea melampyra* bannermani*** (Chapin) 1948 : Ngara, Cuanza Sul.

Specimen

1 ♀ 12 m. S. of Gabela, 16th Sept.

Field Notes

This specimen was collected in the forest.

Systematic Notes

It is not proposed here to go into the vexed question of the taxonomy of the Paradise Flycatchers but in order to discuss the situation that prevails in Angola it is necessary to define the main groups under discussion. For this it is most convenient to follow Mackworth-Praed and Grant (1955 : 223) in considering the group comprised of the forms *plumbeiceps* of Angola and *violacea* Grant & Praed as separate from other forms of *T. viridis*. In these two forms the wings and mantle are cinnamon in colour with no white, the head is light grey with a long crest, the underparts are grey with a considerable amount of white on the abdomen and the under tail-coverts white or washed with rufous ; males have a long tail. The other group with which we are concerned is the generally recognized species *T. melampyra* (= *T. rufocinerea* of Chapin and other authors—see Grant & Mackworth-Praed 1957), comprising the races *batesi* (Chapin) of the Camaroons, *melampyra* Verreaux of the Lower Congo and extreme northern Angola (Quela and Canzele—Traylor *in litt.*) and *bannermani* of north western Angola, south of *melampyra*. *T. m. melampyra* has the wings and mantle a bright orange rufous, the head a deep metallic blue with a short crest, the underparts dark grey with no white on the abdomen, and has deep rufous under tail-coverts and a short tail.

Chapin in his paper on hybridization among the Paradise Flycatchers (1948 : 118) discusses the hybrid population *bannermani*, derived from inter-breeding between the *melampyra* and the *plumbeiceps* groups. He shows *bannermani* to be closer to *melampyra* but showing an approach to the *plumbeiceps* group in having a paler head, longer crest and paler underparts. He indicates that *bannermani* has become sufficiently stabilized to live alongside *plumbeiceps* though ecologically segregated, *bannermani* being found in more wooded or forested habitat while *plumbeiceps* keeps to more open country. All localities from which *bannermani* has been collected lie in the centre of the Escarpment Zone and our single specimen was collected within the escarpment forest. We did not find *plumbeiceps* ourselves in this area but Ansorge collected both forms at Ndala Tando, though there are unfortunately no data on his specimens as to the type of country in which they were obtained. Chapin does not cite actual evidence of the two forms breeding alongside, and, in fact, the majority of *plumbeiceps* from north-western Angola have been collected in the non-breeding season, June to August, when it is known to wander widely. There is, however, a female *plumbeiceps* from Dondo collected by Ansorge in November to support his view and its known breeding range come, very close to the Escarpment Zone at Malanje and Moco. This seems to present an unusual case of two species hybridizing, possibly through some temporary breakdown of ecological barriers, and then at a later date the hybrid population being again divided into two populations, which we now recognize as *bannermani* and *plumbeiceps*, each of which is strongly associated both morphologically and ecologically with one of the parent species although showing some influence of the other parent.

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* Since this was written the specimen in the British Museum alleged to be the type of *melampyra* has been re-examined at the request of Dr. J. P. Chapin, and found not to be the type. It is probable that the name *melampyra* will prove indeterminate : meanwhile it is preferable to use *rufocinerea* for this species.

This factor has been recognized in the discussions on *bannermani* which is accepted as a race of *melampyra* showing an approach to *plumbeiceps*, but it does not seem to have been appreciated that it is also important in considering the status of the Angola population of the *plumbeiceps/violacea* group. A study of all specimens of this group shows that there is great variability in the extent of white on the abdomen and in the amount of rufous in the under tail-coverts but that specimens showing little white and a lot of rufous are most common in Angola and the Belgian Congo and less common eastwards into Nyasaland and southwards into South West Africa. This it seems can be directly attributed to the diminishing of the *melampyra* influence away from the zone of one-time hybridization. Since *plumbeiceps* was described from Malanje I believe it should be recognized as a variable race in which the white of the abdomen is usually rather restricted and the under tail-coverts usually rufous, and that it merges imperceptibly into *violacea* of Nyasaland which has usually more white on the abdomen and in which white under tail-coverts predominate. It seems doubtful if *T. viridis subrufa* (Salomonsen 1949) from the south east Belgian Congo, which was described as having dark cinnamon under tail-coverts distinct from some Malanje specimens in which they were white or yellowish, will be found to differ from a larger Angola series which shows all variations.

It is an interesting point that *plumbeiceps* away from the range of *bannermani* is not apparently confined to more open country since a pair were collected in the Moco forest. Of these the female is unusual in having elongated central rectrices like the male.

118. ***Turdus pelios bocagei*** (Cabanis) 1882 : Angola.

Specimen

1 ♂ Mt. Moco 7,000 feet, 23rd Aug. Wing 132 mm.

Systematic Notes

I have followed Mackworth-Praed and Grant (1955 : 241) in considering *T. pelios* a distinct species from the Olive Thrush, *T. olivaceus*, but believe they are wrong in applying the name *schuetti* (Cabanis) to this species. Professor Stresemann has examined the types of both *bocagei* and *schuetti* and emphasizes that *schuetti* belongs to the woodland species *T. libonyanus* : it should therefore be placed in the synonymy of *T. l. verreauxi* and *T. p. bocagei* be used for the forest bird.

The wing length of *bocagei* is very variable. The difference between the Moco bird and a series from N. Angola in the British Museum was found to be so great that I asked Mr. Traylor for details of specimens in Chicago. From the combined series it is apparent that birds from the high country inland, Moco and Quela, are conspicuously larger than those of the escarpment forests : when the species as a whole is reviewed it may be found necessary to recognize two races in western Angola.

TABLE.—*Wing Lengths of Specimens of Turdus pelios bocagei*

Locality (south to north)	♂	♀	Unsexed
Moco	117, 127, 130, 132	119, 121, 123, 123	—
Gabela	110	111, 119	118
Dondo	119	111	—
Ndalo Tando	116, 117, 117, 117	107, 111	—
Golungo Alto	116	—	—
Canzele	114	109	—
Quela	129	—	—

119. ***Geokichla litsipsirupa stierlingi*** Reichenow 1900 : Iringa, Tanganyika.

Specimen

1 ♀ 5 m. W. of Munhango, 8th Aug.

Systematic Notes

Although the Angola Groundscraper Thrushes have been separated as *G. l. kosteri* (Neumann), on slight differences of size and pattern, I can see no reason to distinguish this specimen from *G. l. stierlingi*.

127. ***Myrmecocichla tholloni*** (Oustalet) 1886.

Specimens

2 ♂ 1 ♀ 30 m. W. of Vouga, 12th Aug.

Field Notes

Thollon's Chat was first seen by the road 50 miles east of Vila General Machado and again on the plains near Vouga, but it proved very wary and difficult to approach. The three birds were finally collected near together, two having been watched for some while. It was found that they made use of the few small trees on the open plains, returning again and again to two or three selected perches after forays on the ground for food. The stomach contents showed this to be largely beetles and grasshoppers but fragments of a small lizard were also noted.

The alarm note was a shrill peep " almost identical with the Kenya Anteating Chat." When the first male was shot the female returned and fluttered about in the vicinity. Earlier on a wounded bird was lost and almost certainly had gone to ground in an antbear hole.

It was noticed that, in life, this chat looks darker than in the hand, appearing to be almost black with contrasting white markings.

130. ***Xenocopsychus ansorgei*** Hartert 1907.

Specimens

1 ♂ 1 ? ♀ 1 Leba, 1st Sept.: 1 ♂ 3 m. SW. of Sá da Bandeira, 6th Sept.

Field Notes

Braun (1956 : 41) has written a full account of his observations on *Xenocopsychus* in the Sá da Bandeira area. We found it, as he did, among the rocks and trees on top of the escarpment (see Plate 5, A) and in the gorge of the stream. We did not find it as shy of sunlight as he led us to expect, the first two being collected in the morning of a sunny day. Two pairs at least lived close to each other on the edge of the escarpment, and a pair when pursued at dusk took at least temporary refuge in the tangled thickets behind. Both the song and the alarm note were heard: the double-syllabled alarm whistle by one bird was frequently answered by a single whistle from the other. They moved and behaved much as a *Cossypha*, and in dimensions and pattern as well have much in common with *Cossypha heuglini*.

The stomach contents were found to contain fragments of both larvae and adult ground-living beetles, Tenebrionidae, Staphylinidae, and a weevil, *Blosyrus*, also fragments of ants.

Systematic Notes

The ♂ from Sá da Bandeira and the unsexed specimen from Leba are notably larger than the other two. Wing 104–106; bill 23, 23; tail 105, 111; against wing 96, 96; bill 21, 22; tail 99, 93 for the specimens from Leba sexed as male and female. Furthermore, there is some difference in tail pattern between the two larger birds and the two smaller; in the larger the black on the outer edge of the outermost rectrices extends about 56 mm. from the tip; in the smaller pair it extends 37–40 mm. from the tip. It seems probable that an error was made in sexing the " male " from Leba and that this difference in size and tail pattern between the two pairs may be due to sexual variation.

132. ***Cossypha polioptera ? polioptera*** Reichenow 1892: Lake Victoria.

Specimens

1 ♂ 2 ♀ Luacano, 2nd Aug.

Systematic Notes

C. p. grimwoodi White, was described from the Mwinilunga district as having a clearer grey head top, and the back and rump less tawny, more olive brown than *polioptera*. With seasonal variation and a certain amount of foxing in old skins it is difficult to place these. They have the head and mantle darker than *grimwoodi*, and the mantle, except in one female which was salted, more olive than available specimens of *polioptera* which may possibly be slightly foxed.

I therefore refer these tentatively to *polioptera* which extends across the continent to northern Angola : possibly the division between the two races may be found to lie along the Congo/Zambesi watershed.

133. (a) ***Cossypha natalensis intensa*** Mearns 1932.

(b) ***Cossypha natalensis larischi*** Meise 1958, p. 73 : Canzele, Cuanza Norte.

Specimens

(*a*) 1 ♂ 1 ♀ Luau R., 29th July : 1 imm. ♀ Luacano, 2nd Aug. (*b*) 1 ♂ 2 ♀ 1 imm. ♀ 12 m. S. of Gabela, 17–18th Sept.

Systematic Notes

The distinctiveness of the north Angola population and variation within *C. n. intensa* have been discussed (Hall 1958 : 154).

138. (a) ***Erythropygia leucophrys munda*** (Cabanis) 1880 : Malanje.

(b) ***Erythropygia leucophrys ovamboensis*** Neumann 1920 : Ombongo, Ovampoland.

Specimens

(*a*) 1 ♀ Quipungo, 29th Aug. (*b*) 1 ♀ E. of Cahinde, 6th Sept.: 1 ♀ 60 m. N. of Lobito on Novo Redondo road, 13th Sept.

Systematic Notes

It would seem that *munda* and *ovamboensis* are ecological races, *munda* being found in the woodlands and *ovamboensis* in the thorn country. Both the Quipungo and Cahinde birds were taken in areas where the two types of country meet, the first in a bush between a pocket of woodland and a pocket of thorn scrub, the second near the foot of the escarpment where stunted Brachystegia and mopane gives way to the semi-desert. This latter specimen has also some intermediate characters being more heavily streaked than is usual for *ovamboensis*, but is considerably paler above and less washed with rufous below than *munda*.

139. ***Erythropygia leucosticta reichenowi*** Hartert 1907 : Canhoca, Cuanza Sul.

Specimen

1 imm. ♀ Chingoroi, 9th Sept.

Field Notes

This elusive scrub robin was never seen, the single specimen being collected in a net set in slender, very close-growing trees with very little undergrowth, near the stream in the forest.

Systematic Notes

This is the most southern record for the species and I believe the first known female of this form. It was compared with two males from northern Angola borrowed from Chicago and was found to be a good match, only a trifle paler on the mantle. It still has some young feathers with rufous edges in the secondaries and wing-coverts.

141. ***Acrocephalus baeticatus cinnamomeus*** Reichenow 1908.

Specimen

1 ♀ Chingoroi, 8th Sept.

Systematic Notes

The three races of Reed Warbler, *baeticatus* (Vieillot), *cinnamomeus* and *suahelicus* Grote, are, at best, only distinguishable in series. This specimen, in moult, is unsatisfactory for comparison but has been identified as *cinnamomeus* by Mr. C. M. N. White, who is preparing a revision of the species.

143. ***Bradypterus mariae boultoni*** Chapin, *Ann. Carn. Mus.* 31, p. 1, 1948: Mombolo, Cuanza Sul.

Specimens

1 ♂ 2 ♀ Mt. Moco 7,000 feet, 16–23rd Aug.

Field Notes

This Forest Warbler was quite plentiful in the pockets of forest, as its voice, a loud " chep, chep " frequently repeated, was heard throughout the day, even when other birds were silent. It was not often seen, and always in thick undergrowth and very near the ground. The stomach contained crickets and other insects.

142. ***Seicercus laurae laurae*** Boulton 1931: Mt. Moco.

Specimens

2 ♂ 2 ♀ 1 Mt. Moco 7,000 feet, 19–22nd Aug. (1 in spirit.)

Field Notes

Two of these were a pair found in thickish forest, the female carrying nesting material of feathers. Another was one of a party of three or four feeding in foliage about ten feet from the ground. The food was found to be larvae and insect fragments.

145. (a) ***Calamocichla gracilirostris winterbottomi*** White 1947 : Manyinga R., Macondo dist., Moxico.

(b) ***Calamocichla gracilirostris cunenensis*** Hartert 1903 : Cunene R., S. Angola.

Specimens

(*a*) 2 ♂ 2 ♀ Lake Dilolo, 3–5th Aug. Wings ♂ 72, 74, ♀ 68, 69. (*b*) 1 ♀ Leba, 30th Aug. Wing 69 mm.

Systematic Notes

I have followed Chapin (1953 : 441) in assigning both these forms of Swamp Warbler to *C. gracilirostris* (Hartlaub). The birds from Lake Dilolo answer the description of *winterbottomi* but are a little larger, the type series having wings of 67–71 mm. The Leba specimen is not strikingly different but is a little paler on the back and is more washed with buff on the flanks and thighs.

147. ***Calamonastes simplex huilae*** Meise 1958, p. 72 : Huila.

Specimens

1 ♀ Mt. Moco 6,000 feet, 24th Aug.: 1 ♀ Vila Flor, 26th Aug. Wings 63, 64 : bill 14 ; tail 46, 48 mm.

Systematic Notes

These Wren-warblers answer the description of Meise's new race, and the characters of these and some specimens from Vila da Ponte, collected by the Visser-Transvaal Museum, had already been observed by Dr. Rudebeck and myself before the publication of Meise's paper.

149. ***Apalis rufogularis brauni*** Stresemann 1934 : Roça Congulu, Cuanza Sul.

Specimens

1 ♂ 2 juv. ♀ 12 m. S. of Gabela, 16–18th Sept.

Field Notes

The adult was collected in the very top of a tall tree by the river ; the others were in the escarpment forest, one being a member of a family party of four in thickish trees about ten feet from the ground.

152. ***Sylvietta r. ruficapilla*** Bocage 1877 : Caconda, Huila.

Specimens

1 ♀ Lake Dilolo, 5th Aug.: 1 ♂ 15 m. N. of Vila Flor, 25th Aug.: 1 ♀ Caconda, 28th Aug.

Systematic Notes

All three specimens vary in the extent of rufous on the neck. The female from Caconda has none and has the thighs also grey ; the male from Vila Flor and a pair from Caconda in the British Museum have a narrow half circle of pale rufous on the neck and pale rufous thighs. The female from Lake Dilolo has a dark rufous patch on the neck and dark rufous thighs. It also has the white of the lores very much reduced, but in all other respects matches in colouring with the topotypical birds. On the limited material available it is not possible to judge the significance of this variation.

154. (a) ***Sylvietta rufescens ansorgei*** Hartert 1907 : Huxe, Benguela.
(b) ***Sylvietta rufescens mossamedes*** Meise 1958, p. 71 : 25 m. S. of Jau, Moçamedes.

Specimens

(*a*) 1 ♂ 1 ♀ 12–15 m. SE. of Benguela, 11–12th Sept. (*b*) 1 Leba, 31st Aug.

Systematic Notes

The possiblity of *Sylvietta rufescens* and *S. ansorgei* being conspecific was suggested by Macdonald & Hall (1957 : 28) when a specimen from Ohopoho, Kaokoveld, was discussed. This specimen showed some intermediate characters, as does the unsexed specimen from Leba. Further similar specimens were examined by Meise who has given them the name *mossamedes*. The Ohopoho bird is in the Transvaal Museum and has not been compared with the Leba bird, but it seems certain that it will also be found to be this race.

155. (a) ***Eremomela icteropygialis puellula*** Grote 1929 : Catumbela, Benguela.
(b) ***Eremomela icteropygialis polioxantha*** Sharpe 1883 : Swaziland.

Specimens

(*a*) 1 ♀ Cahinde, 5th Sept.: 1 ♂ 12 m. SE. of Benguela, 12th Sept. (*b*) 1 100 m. W. of Vila Luso, 8th Aug.: 1 Vouga, 10 or 11th Aug. Wing (*a*) ♂ 50, (*b*) ♀ 53 mm.

Systematic Notes

The series of *puellula* in the British Museum shows that birds from south Angola are rather darker as well as smaller than South West African specimens (wings of 7 ♂ 49–55 ; 6 ♀ 48–53 against 4 ♂ 54–57 ; 9 ♀ 52–57 mm.).

The two specimens of *polioxantha* were unfortunately badly shot and preserved in spirit ; they have since been skinned but are not very satisfactory for comparison. This is unfortunate as they are important specimens showing that grey-backed birds are found well within the range of the green-backed *E. salvadorii* (see species 158) supposed by some authors to be conspecific. There is, however, no question that any green on the mantle might have been lost in the spirit since these were grey when collected, the only green-backed *Eremomela* being obtained later at Vila Flor and recognized then as something new to our collection.

The races *puellula* and *polioxantha* provide examples of strongly differentiated races specialized in thorn and Brachystegia country.

157. ***Eremomela atricollis*** Bocage 1894.

Specimens

2 ♂ 5 m. W. of Vila General Machado, 10th Aug.: 1 ♂ 1 ♀ 15 m. N. of Vila Flor, 25–26th Aug.: 1 ♀ 5 m. S. of Caconda, 28th Aug.

Field Notes

The Black-necked Eremomela was found in fairly tall and in stunted Brachystegia. It was noted to be very active, fossicking for insects with tit-like agility, often upside down. It was once found with a small party of *E. scotops*.

158. ***Eremomela salvadorii*** Reichenow 1891 : Leopoldsville, Belgian Congo.

Specimen

1 ♀ 5 m. N. of Vila Flor, 26th Aug.

Systematic Notes

Specimens of the green-backed species in the British Museum have been obtained at Nova Lisboa, Vila Luso, both by Admiral Lynes, and now at Vila Flor. They establish it as sympatric with *E. i. polioxantha* and as a bird of bushes on the edge of woodlands, thus requiring very similar but possibly more open habitat. There seems no significant difference in colour between the Angola birds and some from Luluabourg in the Kasai, and I follow the authors in considering *E. griseoflava lundae* Grant & Praed, a synonym of *E. salvadorii*.

159. (a) ***Camaroptera brevicaudata sharpei*** Zedlitz 1911 : Damaraland.
(b) ***Camaroptera brevicaudata*** subsp. (?)
(c) ***Camaroptera brevicaudata harterti*** Zedlitz 1911 : Canhoca, Cuanza Sul.

Specimens

(*a*) 1 ♂ Leba, 3rd Sept.: 1 ♂ 1 juv. Chingoroi, 8th Sept.: (*b*) 1 ♂ Luau R., 28th July (and one in spirit). (*c*) 1 ♀ Gabela 17th Sept.

Systematic Notes

The green-tailed form *harterti* with very white underparts is strikingly different from other races of *C. brevicaudata*, all of which have brown or grey-brown tails and are heavily washed with grey or buff on the chest. Its range is apparently restricted to localities on and below the escarpment from Ndala Tando and Luanda to Gabela and the specimens were probably all collected, as ours was at Gabela, in the escarpment or riverine forests. It is the more surprising therefore that other forms have been collected in similar forests at Chingoroi and Canzele, ours from Chingoroi being netted alongside such a typical forest bird as the Wattle-eye, *Dyaphorophia concreta*. The Canzele specimens in the Chicago Museum are those referred by Heinrich (1958 : 349) to *C. b. harterti* and which proved on examination to be *C. b. tincta*.

It seems possible that *harterti* is the true ecological representative of *C. brevicaudata* in the escarpment forests, but that, on the northern and southern edges brown-tailed forms have intruded on its habitat, and it would not be surprising if *harterti* was eventually found as well at Canzele or Chingoroi.

Among the brown-tailed races it has been found, as with many Cisticolas, that there is little or no seasonal variation in some of the tropical forms, but well-marked variation in the sub-tropical forms. *C. b. sharpei* of southern Africa (of which *C. b. beirensis* Roberts, is considered a synonym) is an example of the latter, non-breeding birds having mouse-brown backs and the underparts washed with buff, breeding birds having grey backs and greyish white underparts. North of *sharpei* on the east of the country is *erlangeri* Reichenow, of eastern Tanganyika, with little seasonal change and characterized by very white underparts and a greyish-brown back. North again is *griseigula* with the underparts strongly washed with grey. On the west, north of *harterti*, is the dark grey *tincta* (Cassin), with no seasonal dress. This is found in Gaboon, Cameroons and northern Angola, extending into the northern Congo where it intergrades with East African races (see Chapin 1955 : 317).

However, in central Africa north of the recognizable limits of *sharpei*, west and south-west of *erlangeri* and *griseigula*, and south of *tincta*, there are specimens which represent an intermediate or several intermediate populations. These are similar above to *erlangeri* and *griseigula* in having grey-brown mantles, and below are closest to the breeding dress of *sharpei* but with slightly less grey on the throat and slightly washed with buff on the flanks. There seems to be little or no seasonal change.

Specimens examined which show these characters are as follows:

Angola: 1 ♀ Malanje, 24th Feb.; 1 ♀ Missao de Luz, Jan, coming into breeding condition; 1 juv. ♂ Saurimo, Lunda dist. 20th Dec. (the two latter previously identified as *harterti*, Ibis, 1934 : p. 46). 1 ♂ Luau R., 28th July, not in breeding condition.

Belgian Congo: 1 ♂ Kayoyo (10° 30′ S. 24° 30′ E.), 1st Sept. coming into breeding condition. 1 Kambove, 1st July.

NW. Rhodesia: 1 ♂ Kabompo R., 9th Feb. 1 imm. ♂ Mwinilunga, 9th Jan.

Tanganyika: 1 ♂ Lukolansala R. Western Prov. 20th Nov.; 1 ♂ Mt. Hanang, 11th Feb.; 1 ♀ Usangu dist. 5th Nov.; 2 ♂ 2 ♀ 1 juv. ♂ Iringa uplands, 19th Jan. and 5th March, the March specimens post-breeding.

It will be seen that this is a very inadequate series from widely scattered localities and without proper seasonal representation in any one place, and it may well be that adequate series will show that birds from these localities are not so homogenous as now appears. Until more material is available I do not feel that there is justification for giving them a name.

The adults collected at Chingoroi and Leba are typical of *sharpei* in non-breeding dress.

162. **Cisticola chiniana** near *frater*.

Specimen

1 (♂ on size) Leba, 31st Aug.

Systematic Notes

This specimen is rather darker than *frater* Reichenow, from Damaraland, as are three collected by Lynes in 1931 from the Que R. (14° 30′ S., 14° 30′ E.) which he labelled as " near *frater*."

181. **Hirundo abyssinica unitatis** Sclater & Praed 1918.

Specimen

1 Mt. Moco 7,000 feet, 17th Aug.

Field Notes

This Striped Swallow was observed to be apparently nesting in the cliff face over a waterfall in the mountain forest. This was unexpected as Chapin (1953 : 761) notes that in the Congo it is wanting on all the higher mountains, especially those that are forested.

190. **Ptynoprogne fuligula** near *rufigula*.

Specimen

1 Mt. Moco, 22nd Aug. Wing 121 mm.

Systematic Notes

Chapin (1953 : 744) suggests that Rock Martins from the central highlands of Angola are intermediate between *rufigula* (Fisher & Reichenow) of East Africa and the pale *anderssoni* (Sharpe & Wyatt), of South West Africa. This specimen is true *rufigula* in colour, but is larger, as is *anderssoni*.

192. **Petrochelidon rufigula** (Bocage) 1878.

Specimens

3 ♂ 6 ♀ 20 m. W. of Vila General Machado, 10th Aug. (and one in spirit) ; 1 ♂ 2 ♀ 1 Nova Lisboa, 12–13th Aug.

Field Notes

This cliff swallow was found breeding in a colony under a concrete road bridge. There were about two hundred and fifty nests massed together ; each was a large half sphere approximately 9 inches wide and 4 inches deep with an entrance spout varying greatly in construction but always very wide, about 2 inches across. The nest was lined with fine grass, no feathers. A clutch of two eggs was taken from one nest and a single egg from another. Several pairs of *Micropus caffer* were parasitizing some of the nests. In the Lower Congo *P. rufigula* was found breeding in April (Chapin 1953 : 773).

Systematic Notes

Chapin notes that *P. rufigula* is closely allied to *P. preussi* (Reichenow). Their affinities are further stressed by the eggs, which were examined by Dr. W. Serle, to whom I am indebted for the following notes.

Eggs : (Notes made by Dr. W. Serle, 31.xii.58).

" Eggs ovate, slightly glossy, smooth surface. Ground colour white tinged creamy pink. Spotted and blotched with reddish-brown and chestnut, brown primary and ashy violet secondary markings, both primary and secondary markings being densest about the large end and where they coalesce to form a ring or cup. One egg shows a few black hair lines. They measure 18·2 × 12·9 ; 19·5 × 13 ; 19·3 × 13·1 mm.

"In appearance they closely resemble one type of *Petrochelidon preussi* (Reichenow), from Nigeria, and on the criterion of the egg (size, shape, ground colour, markings, texture etc.) there is no reason why *Petrochelidon rufigula* and *P. preussi* should not be conspecific. On the other hand, these three *P. rufigula* eggs do *not* resemble *Petrochelidon spilodera* eggs from South Africa (of which I have seen many), nor do they resemble the eggs of *Petrochelidon fuliginosa* (Chapin) of the Cameroons.

"The eggs of *P. preussi* and *P. rufigula* are distinctive. I do not know any other African swallows' eggs that resemble them."

199. ***Prionops gabela*** Rand, Fieldiana 39, p. 43, 1957 : 15 km. S. of Gabela.

Specimens

1 imm. ♀ 12 m. S. of Gabela, 20th Sept.: 1 ♀ 40 m. S. of Mumbondo on Gabela-Muxima road, 20th Sept.

Field Notes

The first specimen of this new Helmet Shrike was obtained by Heinrich in " a little region of tangled tropical second growth along the ridge of a higher mountain range." From his subsequent paper (1958 : 128) it seems that he was camped a few miles further up the Cuvo River, nearer Assango, than we were. Our first specimen was obtained also on a ridge above the coffee forest where the trees were less thick. The second was found in the country below the escarpment in the trees of a dry thicket by the road in an area of mixed thickets and cultivation. Both were members of small parties.

Systematic Notes

These are the first known females of this species. They answer the description of the male except that both have some white on the 2nd–6th primaries. This white is confined to very small patches on the inner web ; it is slightly more extensive in the adult, and in the young bird is asymmetrical. It is in no case comparable to the large patches in *P. retzii*.

Signs of immaturity in the Gabela specimen are found in a few brown feathers, very worn, among the fresh black feathers of the head, and in the colours of the iris, bill and legs as compared with the adult.

	Imm. ♀, Gabela	Ad. ♀, Mumbondo
Iris	Yellow	Yellow with red outer ring.
Bill	Red base, orange tip	Red, orange tip to lower mandible.
(In the dried skin the orange of the greater part of the lower mandible of the young bird is very noticeable.)		
Legs	Bright orange-red	Cherry-red.
Eye wattle	Red	Red.

204. ***Laniarius aethiopicus major*** (Hartlaub) 1865 : Elminia, Gold Coast.

Specimens

1 imm. ♂ Luau R., 31st July : 1 ♂ Lake Dilolo, 5th Aug.

Field and Systematic Notes

See next species.

206. ***Laniarius bicolor guttatus*** (Hartlaub) 1865 : Benguela.

Specimens

1 ♂ 2 ♀ 1 imm. ♂ Leba, 31st Aug.–1 Sept.: 1 juv. Chingoroi, 8th Sept.

Field Notes

The relationships and habitats of the Boubou Shrikes were discussed (Hall, 1954), and it was suggested that the different species were more restricted in their choice of habitat in the areas where two species were near neighbours. It was particularly interesting therefore to have my first experience of them in the field in Angola where *L. aethiopicus* and *L. bicolor* adjoin. Disappointingly little was seen of these shrikes in the critical central areas, the only specimen shot being one in the foothills of Mt. Moco which was never recovered from a thick reed-bed in the valley of a stream.

However, in the eastern districts *L. aethiopicus* was found to be an inhabitant of scrubby bushes in the Brachystegia woodlands, as it is in south-western Northern Rhodesia and the Caprivi Strip, where it occurs alongside *L. b. sticturus* Finsch & Hartlaub.

In the west *L. bicolor* was collected at Leba in thick cover by the stream or on the hillside just above, at Chingoroi in cover by the stream, and from a dry tangled thicket in the grass and thorn country above the sea near Novo Redondo. These different habitats in the extreme west conform to the suggestion that the habitats are less specialized away from competition with the related species.

Systematic Notes

The adults of the two species are readily distinguished by the relative whiteness of the underparts, and the observations made in the previous paper on the eye-colour of the two species, was borne out by our specimens ; the adult of *L. aethiopicus* being noted as having the iris " rich dark brown " and those of *L. bicolor* having it " dark brown."

The young birds are harder to distinguish since the pinky tinge on the breast of *aethiopicus* and the pure white of *bicolor* are replaced in the young by a buffy tinge in both species. But, as with the adults, when the feathers of the breast are lifted it will be seen that in *aethiopicus* they become more tinted with colour towards the base, which is black, whereas in *bicolor* they become whiter towards the black base.

Leba lies on the borders of two races, *L. b. guttatus* (smaller with two secondaries usually edged white) and *L. b. sticturus* (larger with three secondaries usually edged white). Two Leba birds have a narrow edge on the third secondary but in respect of size (wings 92–96) are clearly best referred to *guttatus*.

211. ***Tchagra s. senegala*** (Linnaeus) 1766 : Senegal.

Specimens

1 ♂ 1 ♀ Luau R., 27th July : 1 ♀ 40 m. W. of Texeira de Sousa, 31st July : 1 ♀ Mt. Moco 6,000 feet, 18th Aug.

Systematic Notes

Two of these Tchagras are just finishing moult, the other two just starting, so they illustrate well the extremes of seasonal variation. The two fresh birds were found to match well with some fresh specimens from West Africa. I therefore do not recognize *rufofusca* (Neumann), described from north Angola as distinct from the nominate race.

214. ***Chlorophoneus multicolor batesi*** Sharpe 1908 : R. Ja, Cameroons.

Specimens

1 ♂ 1 imm. ♂ Gabela, 16th Sept.

Systematic Notes

Moreau & Southern (1958) discuss colour variation in this and the following species of bush-shrike. The adult bird is in their " Yellow D " phase (p. 316) as are all others that were examined from north Angola : the young bird has yellow, not orange, underparts, light tips to the wing-coverts, light edges to the gape, and was noted as having a dark brown, not a deep purple, iris.

In their paper no mention was made of differences in size between Angola and Cameroon birds but later Moreau, examining specimens with me, found that those from Angola, including some borrowed from Chicago, have smaller bills. The bills of two from Gabela are particularly small (19, 20 mm.), four from further north in Angola have them slightly larger (20–21 mm.), while the bill in Cameroon birds is 21–23 mm. and deeper in proportion.

There is also a tendency for Angola birds to have the grey of the crown and hind neck more sharply demarcated from the mantle than in Cameroon birds, but this is not constant.

215. ***Chlorophoneus nigrifrons manningi*** (Shelley) 1899.

Specimen

1 imm. ♂ Luau R., 29th July.

Field Notes

Moreau and Southern (1958 : 308) found that the population of the Blackfronted Bush-Shrike in Northern Rhodesia was less restricted ecologically than others. This was confirmed by our specimen which was found not far from the river in light Brachystegia woodland, and not in forest, as is more usual.

217. ***Telephorus viridis*** (Vieillot) 1817.

Specimens

1 ♂ 1 ♀ Chingoroi, 9–10th Sept. Wing ♂ 90, ♀ 86 mm.

Field Notes

Both of Perrin's Bush-Shrikes were collected, one being netted, in thick undergrowth of the forest. The call was described as " not unlike a francolin call, cut off very short. When hopping about utters a sharp but muted ' chunk . . . chunk . . . chunk.' "

Systematic Notes

The race *T. v. vieiriae* White, was described from eastern Angola on slight differences in size and colour in comparison with the typical race, in particular on evidence of sexual dimorphism not believed to exist in birds of western Angola. Examination of the series in the British Museum shows that there are differences between the sexes in both populations, the female always having the red and green of the throat and underparts paler and duller. Furthermore, these two birds are larger than those previously recorded from the west and similar in size to White's series. I can therefore see no grounds for recognizing *T. v. vieiriae.*

218. ***Malaconotus hypopyrrhus interpositus*** Hartert 1911 : 40 m. W. of Baraka, Lake Tanganyika.

Specimens

1 ♂ Luau R., 29th July : 1 ♀ 5 m. W. of Munhango, 9th Aug.

Systematic Notes

The taxonomy of the Grey-headed Bush-Shrike has been confused by differences of opinion on the correct use of *blanchoti* Stephens, *poliocephalus* (Lichtenstein), or *hypopyrrhus* (Hartlaub), as the specific name, and on the importance of an orange wash on the underparts, and of a white circle round the eye as taxonomic characters.

I follow Grant & Mackworth-Praed (1958 : 19) in using *hypopyrrhus* as the specific name, and follow Chapin (1954 : 42) in recognizing geographical as well as individual variation in the amount of orange wash on the underparts. I do not however, agree with Chapin's treatment of the Angola birds, all of which he calls *monteiri*, distinguishing them from *interpositus* of Rhodesia by the lack of any orange wash below on the majority of specimens. The white circle round the eye, characteristic of the type of *monteiri* (Sharpe), from near Luanda, and the type of *perspicillatus* (Reichenow) from Cameroon Mt. he considers an abnormal character of no taxonomic significance.

Other specimens with this character are from Dondo and Ndala Tando (in the British Museum), Gabela and " Bucaso " (in Chicago). With the exception of Cameroon Mt. and " Bucaso ", which has not been located, all these places are along or below the escarpment in north-western Angola, and all have riverine and escarpment forest rather than woodland. All other specimens examined from Angola in Chicago or London have been taken from above the escarpment in more predominantly woodland areas, and have the white on the face variable and restricted to areas between the eye and the bill, or on the lores.

There may thus be an ecological as well as morphological difference between the birds with the white ring and those without and, in my opinion, the name *monteiri* should be used only for those with this character. The race therefore has a restricted range in north-west Angola and possibly a discontinuous distribution north to Cameroon Mt. (see Serle 1954 : 72). The colour of the underparts of *monteiri* is variable, the Dondo and Ndala Tando specimens have an orange wash, the others being clear yellow.

All other specimens from Angola, without the eye-ring, I would include with *interpositus*, at least for the present, though noting that the orange wash commonly found in specimens in the east of the range becomes less frequent and less pronounced in specimens in the west.

In studying these shrikes I am indebted to Dr. A. L. Rand for a copy of his notes on the species and details of specimens in Chicago.

225. **Neocichla g. gutturalis** Bocage 1871 : Huila.

Specimens

2 ♂ 2 ♀ 48 m. SW. of Caconda, 28th Aug. (one in spirit).

Field Notes

For some distance along the Caconda-Quipungo road these Babbler-Starlings were common, flying up from the roadside into bushes and low branches when disturbed by the car. This was in the area of leafless Brachystegia-type woodland mentioned in the discussion on vegetation.

Systematic Notes

These are the first specimens of the nominate race in the British Museum. In comparison with *N. g. angusta* Friedmann, they seem to have the head and throat a paler, clearer grey as well as having larger white tips to the tail.

228. (a) **Lamprotornis m. mevesii** Wahlberg 1857 : Okavango, N. Bechuanaland.
(b) **Lamprotornis mevesii benguelensis** Shelley 1906 : Capangombe, S. Angola. (= *L. m. purpureus* auct.)

Specimens

(*a*) 1 ♂ 25 m. E. of Sá da Bandeira 4,900 feet, 27th Aug.: 1 ♂ 10 m. E. of Cahinde 3,000 feet, 6th Sept. (*b*) 1 ♀ 15 m. S. of Quilengues, 3,900 feet, 7th Sept.

Systematic and Field Notes

The two races of Long-tailed Starling are clearly differentiated in the blue or bronze sheen of the whole plumage and none of the specimens examined show signs of intergradation. The boundary between them seems interesting following the discussion on the three avifaunal zones in Angola, for the bronzy *L. m. benguelensis* seems to be restricted to what might be termed the southernmost tip of the Escarpment Zone, a narrow tongue of rather richer vegetation lying between one thousand and three thousand five hundred feet with the coastal semi-desert on the west and the Brachystegia woodland on the east. Specimens of *benguelensis* have been obtained at Catengue, near Chingoroi, Quilengues, Vila Arriaga and Capangombe. Quilengues lies more than halfway along the Sá da Bandeira to Chingoroi road which descends gradually with the vegetation becoming progressively richer and more varied northwards. Vila Arriago and Capangombe lie in fertile pockets at the base of the Chela escarpment but bordered westwards by the desert.

L. m. mevesii on the other hand has a widespread distribution in the Mopane belt from Nyasaland westwards, and it is confined in Angola to the less arid parts of the Acacia Zone. It has been collected at Jau, Humbe, Chipopia, Mulondo and Mupa. The specimen collected east of Cahinde was one of a number seen on the road down the escarpment, where there was a light covering of mixed bush and stunted trees including Mopane. Although Cahinde lies like Capangombe at the foot of the escarpment, and is only forty miles south, it has not the same rich vegetation and the associations of all species collected there are with the Acacia Zone.

It should be noted that some of the specimens collected by Monard (1954 : 83, 84) were examined with Captain Grant in 1957 through the kindness of the Director of the Musée d'Histoire Naturelle, Chaux de Fonds. Those from Mupa and Mulondo identified as *purpureus* were found to be *L. m. mevesii*, and samples of those identified as *mevesii* were found to be *L. australis*.

231. (a) **Zosterops senegalensis quanzae** de Schauensee 1932 : Upper Cuanza R.
(b) **Zosterops senegalensis heinrichi** Meise 1958 : Canzele, Cuanza Norte.
(c) **Zosterops senegalensis quanzae ≷ anderssoni** Shelley.

Specimens

(*a*) 1 Mt. Moco 6,500 feet, 15th Aug.: 1 ♀ 25 m. N. of Quipeia, 14 Aug. (*b*) 1 ♀ 12 m. S. of Gabela, 19th Sept.: 1 ♂ 28 m. N. of Vila Luso, 8th Aug. (*c*) 1 ♂ Leba, 30th Aug.

Systematic Notes

Identifications have been made on the basis of Moreau's paper (1957). These specimens have interest in filling some of the gaps that were then noted. The Moco and Quipeio birds have the characteristic dull colouring and large size (wing 65, 62) of typical *quanzae*. The Gabela and Vila Luso birds are a shade brighter, particularly on the throat and tail-coverts, and the Gabela bird on the forehead. They are close to, but a little more olive than, the Ndala Tando birds quoted by Moreau which have since been named *heinrichi*.

The Leba bird is altogether brighter below, matching in this respect a topotypical *anderssoni* from Elephant Vley, but being rather darker above and larger (wing 61).

232. **Nectarinia kilimensis gadowi** Bocage 1893 : Galanga, Benguela dist.

Specimens

1 ♂ Vila Flor, 13th Aug.: 9 ♂ 1 imm. ♂ 1 ♀ Mt. Moco 6,000–7,000 feet, 15–21st Aug.: 1 ♂ 2 imm. ♂ 1 ♀ 1 imm. Nova Lisboa, 13–14th Aug.

Field Notes

This sunbird was common on Mt. Moco at all levels, feeding on *Erythrina* and *Loranthus*. Stomach contents included spiders, *Coleoptera*, *Diptera*, and hover-flies. Its call was noted as being exactly like that of the nominate race.

233. **Nectarinia bocagei** Shelley 1879 : Caconda, Huila dist.

Specimens

1 ♀ 3 imm. ♀ near Vila Flor, 13–14th Aug.: 1 ♂ near Luimbale, 25th Aug.

Field Notes

Bocage's Sunbird was rare. It was once found feeding on *Erythrina* with *Cinnyris oustaleti* and *Chalcomitra senegalensis*, and once on red *Loranthus* in Brachystegia woodland.

237. ***Cinnyris o. oustaleti*** (Bocage) 1878 : Caconda, Huila dist.

Specimens

1 ♀ 1 imm. ♀ Nova Lisboa, 12th Aug.: 1 ♂ 43 m. W. of Vouga, 12th Aug.: 2 ♂ 1 imm. ♀ near Vila Flor, 13–26th Aug.: 4 ♂ 1 juv. Mt. Moco 6,000–6,500 feet, 15–24th Aug. 1 imm. ♀ near Luimbale, 25th Aug.

Field Notes

Found feeding on orange-red gladiolis in the Brachystegia woodland on Moco, and on *Albizia* trees at Luimbale. Its food contained seeds, spiders, beetles and Lepidoptera larvae.

Systematic Notes

The seven males, including one in which the skull was not fully ossified, are fairly uniform in appearance with a few metallic feathers on the head and mantle and the metallic plumage below confined to the centre of the throat and chest. In four of the specimens sheath feathers of metallic plumage were found on the chest and mantle; in three, including the immature bird, the wings and tails are in moult, in the others they are fresh. The adult female is moulting wings and mantle. Williams (1955) discusses the moults and plumages of this species, finding that the moult from eclipse to metallic plumage is complete, including wings and tail, but that the wings and tail are not moulted after breeding. It would seem therefore that the males collected are moulting into breeding dress.

The finding of these males concurrently with young birds with skulls 10 % or 20 % ossified suggests a protracted breeding season.

The identification of the juvenile from Moco is not certain, no comparable specimens being available.

246. (a) ***Anthreptes collaris somereni*** Chapin 1949 : Anda, Lake Azingo, Gaboon.

(b) ***A.c. phillipsi*** White 1950 : Lofu R., N. Rhodesia.

Specimens

(*a*) 1 ♂ 1 ♀ 12 m. S. of Gabela, 15–16th Sept. (*b*) 1 ♂ 1 ♀ Luau R., 27–29th July; 1 imm. ♂ 1 imm. ♀ Lake Dilolo, 5th Aug. 1 ♂ 45 m. W. of Vila Luso, 8th Aug.

Systematic Notes

The adult female from the Luau River has the grey throat and chest characteristic of *phillipsi* well marked. The Gabela pair have been identified as *somereni* on locality. In colour they seem indistinguishable from *zambesiana* (Shelley), though they are smaller. Both are bright clear yellow below, without much olive wash on the flanks, and the female has a pale whitish-yellow throat. Comparison between *somereni* and *zambesiana* is a little difficult on available skins in the British Museum since most of those of *somereni* are small, rather pinched skins which exaggerate the dusky flanks and hide the clear yellow of the tummy ; most of those of *zambesiana*, and the Gabela pair, are well filled-out skins which show off the yellow. It seems that there may not be such clear-cut differences between the two races as appears from this series.

252. ***Passer griseus griseus*** (Vieillot) 1817.

Specimen

1 ♂ 12 m. S. of Gabela, 17th Sept. Wing 78, bill 15 mm.

Field and Systematic Notes

See next Species.

253. ***Passer diffusus georgicus*** Reichenow 1904 : Damaraland.

Specimen

1 ♀ Leba, 31st Aug. Wing 78, bill 13·5 mm.

Field and Systematic Notes

The relationship between the two forms of grey-headed sparrow found in coastal Angola has been discussed by Benson (1956) and by White & Moreau (1958), and the authors differ in their views as to whether the two forms can be regarded as conspecific. The two specimens collected conform with Benson's conclusions on the ecological segregation of the forms in western Angola, since the male *griseus* was obtained in the vicinity of native huts in a clearing in the coffee forest, while the female *diffusus* was found in a mountain valley some distance from habitation.

The Leba bird, like others of *diffusus* from Angola, noted by White & Moreau, is small and its bill is horn-coloured, paler below, with a yellow gape. The Gabela *griseus* is also short-winged in comparison with other Angola specimens noted, but has a heavy bill which is black.

257. ***Ploceus temporalis*** (Bocage) 1880.

Specimens

1 ♂ 1 (with nest), Saiangikilo R., 40 m. W. of Munhango, 9th Aug. Wing 81–84 ; bill 19 ; tail 44–45 mm. Bill black ; legs pale reddish-horn ; iris cream.

Field Notes

This rare weaver was only encountered once at a place where the road crossed the river in the centre of an open dambo. The nest, which is unused, was hung in elephant grass beside the river. (Plate 5 B, and 6).

Nest. The nest has been examined by Professor and Mrs. N. E. Collias of the University of California, particularly in respect of the possible relationship of *P. temporalis* with *P. capensis.* I am grateful to them for the following comments, and for the photograph.

" The nest is typically ploceine in its use of green, more or less flexible and interwoven materials. It is a typical *Textor* (*Ploceus*) nest in its ovoidal shape, pensile attachment, ventral entrance, and presence of a special ceiling put in before the nest is lined below. The nest you sent us is unlined and apparently never contained eggs. It belongs to the same size class as nests of *Textor cucullatus, T. spekei* and *T. capensis* and not to the size class of nests of the smaller *Textors.*

" The nest has one specialized feature, unique so far as we know, among nests of the Plocinae. This is the extensive use, for construction of the outer shell, of grass culms from which the flowering tops have apparently been snipped off.

" But on the whole the nest is a primitive one for a Textor, in various ways : loose, untidy weaving, use of grass stems in the outer shell, loose fastenings of individual pieces of nest material as well as loose attachments to the support, irregular ceiling of narrow sections of leaf blade, absence of longitudinally-stripped pieces of leaf blade, and in the occasional presence in the ceiling of grass heads (identified as *Pennisetum* for us by our Botany Department).

" In many of these features the nest resembles most closely that of *Textor spekei* of East Africa. However, the poor ceiling of narrow bits of grass blade seemed to us to be most like that of a young male *T. cucullatus.* In the presence of grass heads in the ceiling it resembles the nests of *Othyphantes, Textor rubiginosa* and *Textor xanthops* ; however, it lacks the abundance of grassheads that is found in the ceiling of these weavers.

" The nest of *Ploceus temporalis* does not seem to us to closely resemble the one nest of *Textor capensis* that we have been able to examine closely . . . This *capensis* nest had the outer shell built of grass leaf strips and palm strips rather than grass stems. It had the ceiling made not only of broad (1 cm.) grass-leaf sections but also of pine needles and cypress branchlets. We recognize, of course, that a nest is only one clue to the taxonomic affinities of birds."

Systematic Notes

Having regard to Professor Collias's comments on the differences between the nests of *P. capensis* and *P. temporalis* as well as to the differences in the bills of the two forms, I do not feel that *temporalis* should be regarded as a race of *capensis*, at least until more is known of its field characters.

The unsexed specimen is a good match with the plate in Shelley (1905 : pl. 41) ; both from its size and colour there is little doubt that it is also a male. The other specimen differs in having the olive of the ear-coverts extending on to the chin and centre of the throat making a tongue of dark colour sharply defined from the yellow of the underparts.

258. ***Ploceus xanthops*** (Hartlaub) 1862: "Angola" = Lower Cuanza River (see below).

Specimens

1 ♂ 2 ♀ Mt. Moco 6,000–7,000 feet, 15–22nd Aug. 2 ♂ Leba, 30th Aug.–3rd Sept. 1 ♀ Chingoroi, 8th Sept.

Systematic Notes

The type locality of *Ploceus xanthops* is given only as "Angola." The original description however is among notes on a small collection made by Monteiro of birds from the coastal areas of north Angola. Definite localities are given for other species, either Cuanza River, Cambambe or Massangano, while the weaver is noted as being "common everywhere . . . particularly over water." It seems that the type locality can therefore be usefully restricted to the Lower Cuanza River and specimens collected from Luanda, Dondo and Vila Salazar can be considered as typical.

This is important since examination of skins in the British Museum, and some from Chicago, show that there is considerable geographical variation within Angola, particularly in the females. The variation is particularly interesting since it follows exactly that found in the Zosterops of Angola. Specimens of typical *xanthops* in the north are rather a yellow green matching the Zosterops described by Moreau (1957 : 372) as intermediates between *Z. s. kasaica* and *Z. s. quanzae* and since named as *heinrichi* Meise (1958 : 80). Those of the Benguela highlands are a darker and duller green, matching *Z. s. quanzae*, while those of the south are brighter, more washed with yellow as is *Z. s. anderssoni*.

When specimens of *Ploceus xanthops* from the rest of Africa were examined, including some borrowed from Pretoria, it was found that this variation in Angola represented the extremes of variation in colour found throughout the continent. The populations of north-eastern Africa, which have sometimes been separated as *camburni* (Sharpe), are brighter and more yellow than typical *xanthops* but similar to the southern birds. The populations of southern Africa, *jamesoni* (Sharpe), are very slightly greener and duller than typical *xanthops* with usually slightly less suggestion of dark streaks on the mantle but not so green or dull as the highland birds of Angola. Most specimens from central Africa match typical *xanthops*, but occasional birds, nearly all of which are from highlands of either southern Tanganyika or Nyasaland, are dull and green, very close to the highland birds of Angola. This is again consistent with Moreau's findings on dark populations of Zosterops at higher altitudes (loc. cit.: 370).

In view of the sporadic distribution of darker and brighter populations it is difficult to see how any races can be recognized on colour differences. In size the wing measurements of all males examined are between 86 and 96 mm. and all females between 80 and 92 mm. with the exception of three from Maun and Lake Ngami, the male of which has a wing of 102 and the females 92 and 94. The name *maunensis* (Roberts), was given to birds from Maun and from the Chobe River ; the latter are no larger than typical *xanthops* so that if *maunensis* is to be considered distinct from *xanthops* it must be restricted to Lake Ngami. In my opinion it is hardly consistent in an admittedly variable species to single out the characters of this one population for recognition by name.

The following table shows that there are other local variations in size but none of any significance. An attempt has also been made in the table to indicate the colour variation in the populations though it must be appreciated that there is also considerable individual variation particularly in the amount of yellow on the forehead of males.

TABLE.—*Populations of* Ploceus xanthops

			Wing length		
Area			♂	♀	Colour
(1) Angola, north	12 ♂	7 ♀	86–93	80–85	Yellow green.
(2) „ highlands	3 ♂	5 ♀	90–91	82–89	Dull green.
(3) „ south	10 ♂	6 ♀	88–94	81–90	Bright yellow green.
(4) N. Rhodesia and S. Belgian Congo	10 ♂	7 ♀	92–96	84–90	As (1) or between (1) and (3).
(5) Nyasaland and northern P.E.A.	27 ♂	26 ♀	88–95	84–90	As (1), occasionally near (2).
(6) S. Tanganyika (highlands)	2 ♂	5 ♀	90–92	86–88	Slightly paler than (2).
(7) Rest of Tanganyika	9 ♂	3 ♀	90–97	88–89	As (3).
(8) Kenya and Uganda	21 ♂	12 ♀	91–97	86–92	As (3), occasionally near (2).
(9) P.E.A. and S. Rhodesia	5 ♂	3 ♀	89–94	84–92	Between (1) and (2), slightly less streaky.
(10) Southern Africa	4 ♂	4 ♀	90–94	84–91	As (9).
(11) Chobe R. and Caprivi	3 ♂	4 ♀	93–94	85–89	As (9).
(12) Lake Ngami	1 ♂	2 ♀	102	92–94	As (1).

264. ***Euplectes aurea*** Gmelin 1789.

Specimen

1 ♂ 12 m. E. of Benguela, 12th Sept.

Systematic Notes

This male is in very fresh non-breeding dress ; it appears identical in plumage with females.

Cryptospiza r. reichenovii (Hartlaub) 1874

Specimens

1 ♂ 1 ♀ 1 imm. ♂ 12 m. S. of Gabela, 17–18th Sept.

Field Notes

Heinrich also found the Crimson-wing in the forest of Gabela but it has not been recorded from elsewhere in Angola. That it should be found here, and not in the montane forest on Moco, is surprising since it is more usually a mountain bird, being found on Cameroon Mountain and the highlands from Ruwenzori to Mashonaland, though descending to the coastal plain at Amani.

Systematic Notes

Chapin (1954 : 486) notes the difficulties of distinguishing between the races of this species. From examination of the series in the British Museum the only geographical variation apparent is that the breasts and abdomens of all specimens from the Cameroons, Ruwenzori, Mufumbiro Volcanoes and Angola are more washed with orange, less green, than in specimens from Tanganyika, Nyasaland and Portuguese East Africa. I would recognize therefore only the two races *C. r. reichenovii* and *C. r. australis* Shelley.

281. ***Clytospiza c. cinereovinacea*** (Sousa) 1889 : Quindumbo, Benguela dist.

Specimens

3 ♂ 1 ♀ 3 imm. 1 juv. ♂ Mt. Moco 6,000–7,000 feet, 15–24th Aug. (and one in spirit).

Field Notes

This Twin-spot was found to be common on Mt. Moco at all levels, in the long grass of the steep mountain gullies along with *Cisticola emini*.

283. (a) ***Estrilda astrild niediecki*** Reichenow, *Orn. Mon.* 24, p. 168, 1916 : Namwala, NW. Rhodesia.

(b) ***E. astrild angolensis*** Reichenow 1902 : Malanje.

Specimens

(*a*) 1 ♂ Vouga, 11th Aug. (*b*) 1 ♂ 1 Mt. Moco 6,000 feet. Wing (*a*) 1 ♂ 50. (*b*) 1 ♂ 49 : tail (*a*) 1 ♂ 51, (*b*) 1 ♂ c. 42 (moult) 41 mm.

Systematic Notes

The Vouga Ruddy Waxbill has light barring and a long tail and is readily identified with the race *niediecki* (synonym *ngamiensis* Roberts) of Barotseland and Bechuanaland rather than with the short-tailed, heavily barred *angolensis*. This represents a considerable extension to the known range of the southern race.

299. ***Fringillaria capensis nebularum*** Rudebeck, *Bull. B.O.C.* 78, p. 129, 1958: Lucira, 130 m. N. of Moçamedes.

Specimen

1 ♀ Leba, 1st Sept.

Systematic Notes

This specimen was found to match well with the type series of the new Angola race.

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APPENDIX 1

Collecting Localities in Angola Outside the Route of the Expedition

Finding the exact location of many collecting localities in Angola has been made difficult over the last fifty years by changes of names for many of the principal towns, changes of provincial boundaries, and changes of spelling. Furthermore, maps are variable and frequently inaccurate and the same name may have been given to several places. In working on the birds of Angola the following works have been particularly useful in plotting distribution combined with the Carta de Angola, published by the Junta das Missões Geográficas e de Investiyações do Ultramar, 1956, scale 1/2,000,000.

Chapin 1954 : 639–738.
Heinrich 1958 : 135.
Monard 1934 : 5–6.
Reichenow 1902 (for all old names).
Gazeteer No. 20, United States Board on Geographic Names, Angola 1956.

In the list that follows of places in Angola mentioned in this paper outside the route of the expedition, the latitude and longitude have been taken from one or other of these sources, the spelling from the U.S. Gazeteer, and the districts as marked on the 1956 map.

Places in Angola Mentioned in the Paper Outside the Route of the Expedition

Ambaca = Camabatela.
Amboim = Gabela (not Porto Amboim).

Bailundo = Texeira da Silva.
Bailundo highlands ; surrounding highlands, west to Mt. Moco.
Biballa = Vila Arriaga, Moçamedes.
Bucosa—not located.
Bulabula plains = Vouga plains.

Cabeça de Ladroes	13° 16′ S. ;	14° 15′ E.	Benguela.
Camabatela.	8° 30′ S. ;	15° 15′ E.	Cuanza Norte.
Cambambe.	9° 30′ S. ;	14° 30′ E.	Cuanza Sul.
Canhoca.	9° 15′ S. ;	14° 41′ E.	Cuanza Sul.
Canzele.	8° 17′ S. ;	15° 11′ E.	Cuanza Norte.
Capangombe.	15° 05′ S. ;	13° 08′ E.	Moçamedes.
Cassongue.	11° 53′ S. ;	15° 02′ E.	Cuanza Sul.
Catengue.	13° 02′ S. ;	13° 46′ E.	Huila.
Catumbela.	12° 25′ S. ;	13° 34′ E.	Benguela.
Chela escarpment.	W. of Sâ da Bandeira, Huila/Moçamedes border.		
Chipepe.	12° 02′ S. ;	14° 55′ E.	Cuanza Sul.
Chipopia.	14° 53′ S. ;	15° 02′ E.	Huila.
Dondo.	9° 38′ S. ;	14° 25′ E.	Cuanza Sul.
Duque de Bragança.	9° 06′ S. ;	15° 57′ E.	Malanje.
Galanga.	12° 04′ S. ;	15° 08′ E.	Benguela.
Hanha.	13° 18′ S. ;	14° 10′ E.	Benguela.

Huambo = Nova Lisboa.

Humbe.	16° 40′ S. ;	14° 55′ E.	Huila.
Humpata.	15° 02′ S. ;	13° 24′ E.	Huila.

Huxe = Uchi.

Jau.	15° 12′ S. ;	13° 31′ E.	Huila.

Lebule = Sandula.			
Lucira, 130 m. N. of Moçamedes.			
Luimbale.	12° 15′ S. ;	15° 19′ E.	Huambo.
Lunda district, North-east Angola.			
Luando R.			Malanje.
Macondo.	12° 35′ S. ;	23° 44′ E.	Moxico.
Malanje (Malange).	9° 30′ S. ;	16° 20′ E.	Malanje.
Manyinga R. Macondo.			Moxico.
Massangano.	9° 37′ S. ;	14° 15′ E.	Cuanza Norte.
Missao de Lus, Vila Luso.			Moxico
Mombolo plateau.	11° 47′ S. ;	14° 33′ E.	Cuanza Sul.
Mt. Soque.	12° 21′ S. ;	15° 02′ E.	Benguela.
Mulondo.	15° 40′ S. ;	15° 15′ E.	Huila.
Mupa.	16° 15′ S. ;	15° 40′ E.	Huila.
Ndala Tando = Vila Salazar.			
Ngara (Negara).	11° 23′ S. ;	14° 11′ E.	
Pungo Andongo.	9° 40′ S. ;	15° 35′ E.	Malanje.
Que R.	14° 30′ S. ;	14° 30′ E.	Huila.
Quela.	9° 16′ S. ;	17° 02′ E.	Malanje.
Quiculungo.	8° 31′ S. ;	15° 19′ E.	Cuanza Norte.
Quindumbo.	12° 28′ S. ;	15° 03′ E.	Benguela.
Roça Congulu.	10° 41′ S. ;	14° 14′ E.	Cuanza Sul.
Sandula.	12° 15′ S. ;	15° E.	Cuanza Sul/Huambo border.
Saurimo.	9° 39′ S. ;	20° 24′ E.	Lunda.
Silva Porto (Bihe).	12° 22′ S. ;	16° 56′ E.	Bié.
Texeira da Silva.	12° 12′ S. ;	15° 52′ E.	Huambo.
Uchi.	12° 40′ S. ;	13° 23′ E.	Benguela.
Vila Arriaga.	14° 46′ S. ;	13° 21′ E.	Moçamedes.
Vila da Ponte (Vila Artur de Paiva).	14° 28′ S. ;	16° 20′ E.	Huila.
Vila Salazar.	9° 18′ S. ;	14° 54′ E.	Cuanza Norte.

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PLATE 5

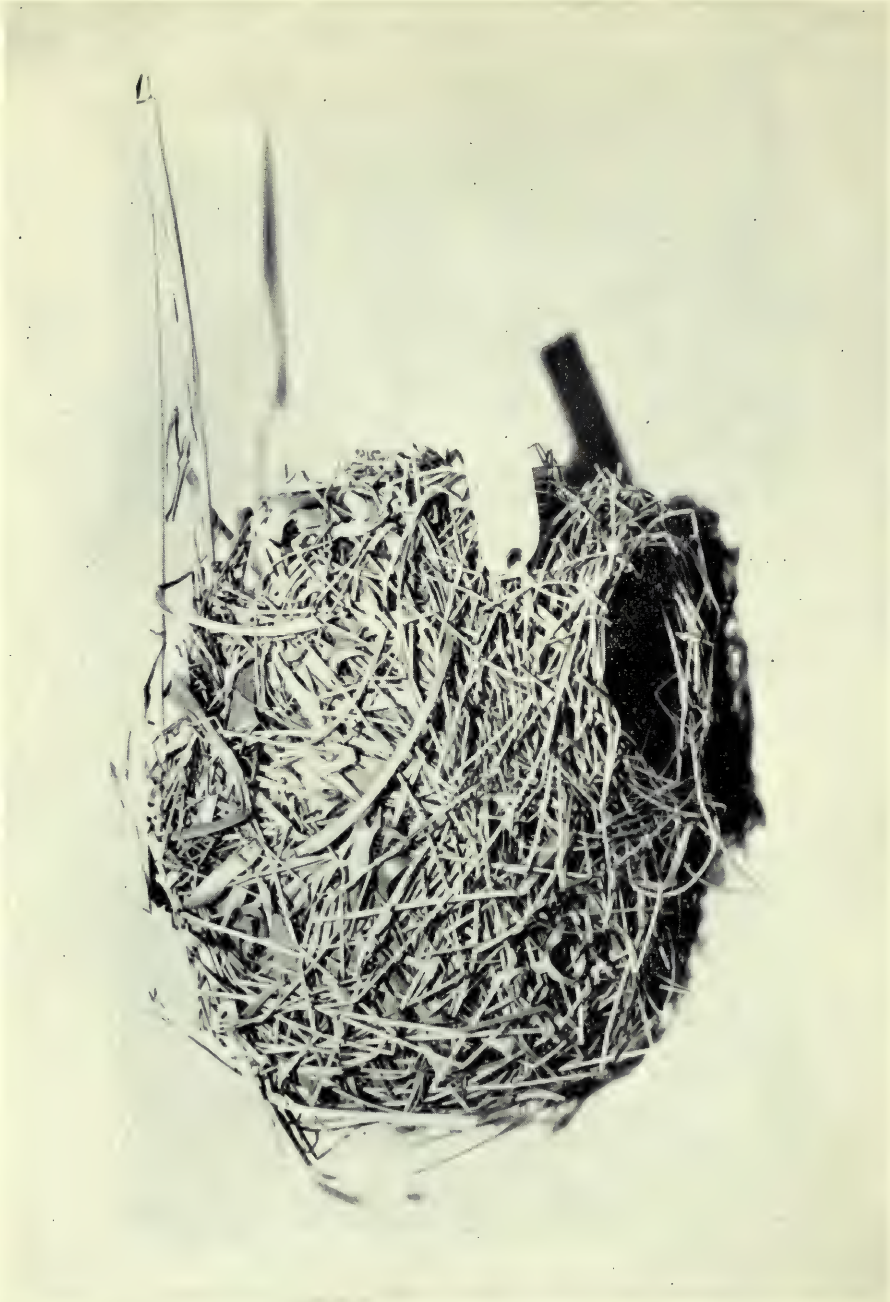
A. Escarpment at Leba. Habitat of *Xenocopsychus ansorgei*.
B. Dambo 40 miles west of Munhango, with nests of *Ploceus temporalis*.

PLATE 6

Nest of *Ploceus temporalis* (Photo. N. E. Collias)

A

B



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